

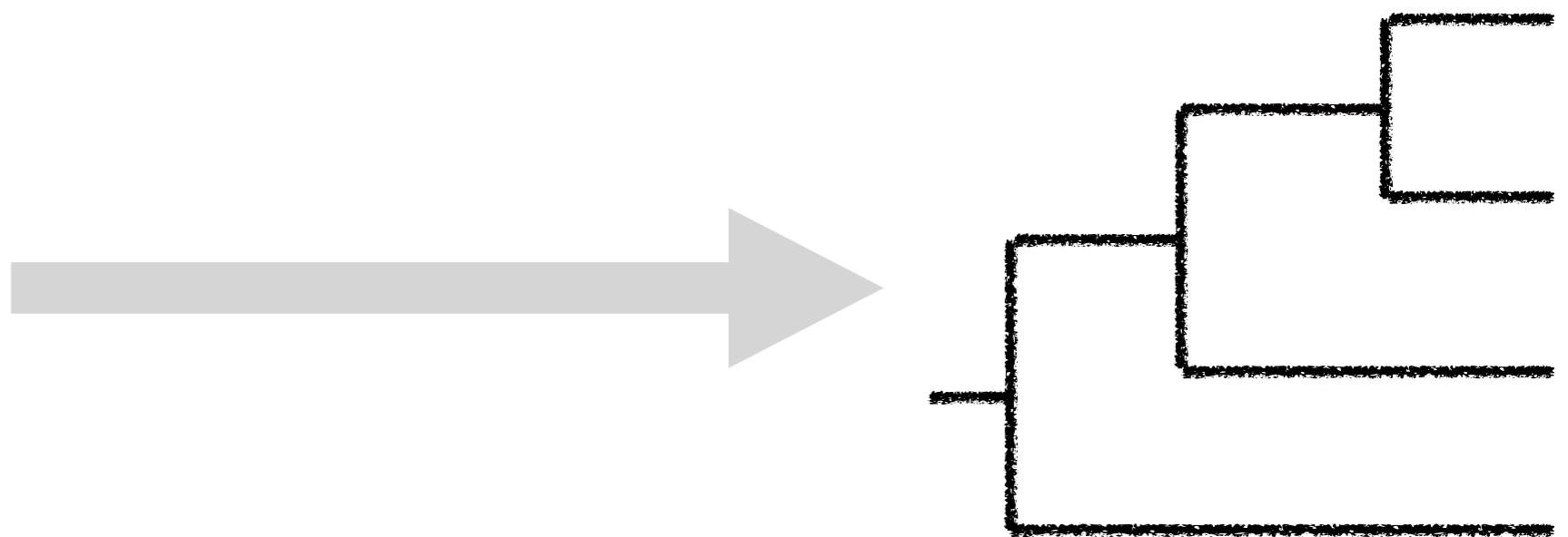
Lecture 14

Coalescent-based methods
Botany 563 – Spring 2021

- **Previous class check-up:**
 - We studied Bayesian phylogenetic inference
 - We practiced on MrBayes and/or PhyloBayes
- **Learning Objectives:** At the end of today's session, you will be able to
 - Explain the coalescent model on a species tree
 - Explain the coalescent model on a species network
 - Explain the steps in coalescent-based methods and the comparison with concatenation approaches
- **Pre-class work**
 - Read HAL 3.1 and 3.3

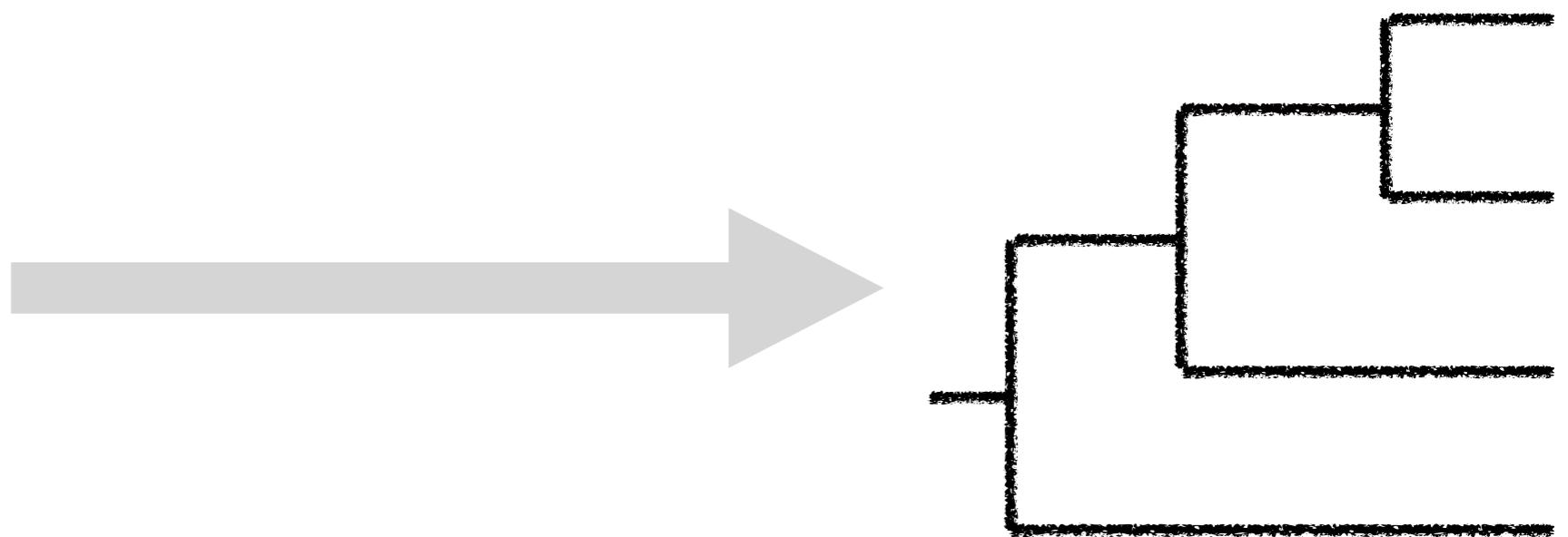
Phylogenetic inference

AAGTCTAG
AAGTCTAG
AACTCTAG
AATTCTAG

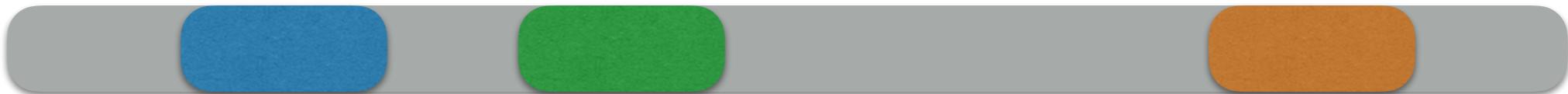


Phylogenetic inference

AAGTCTAG
AAGTCTAG
AACTCTAG
AATTCTAG



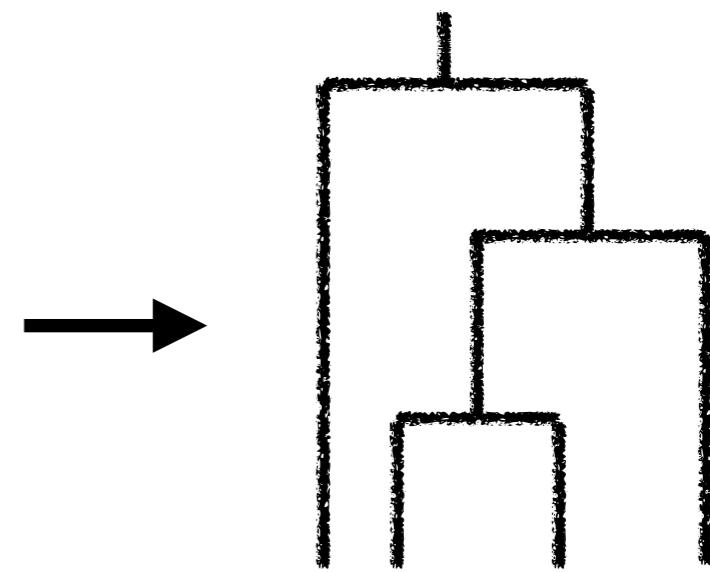
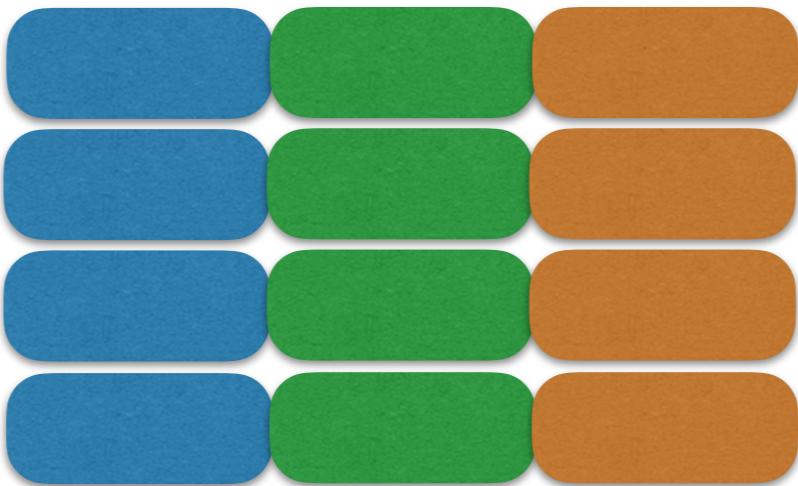
Gene
Locus
Region
Whole genome



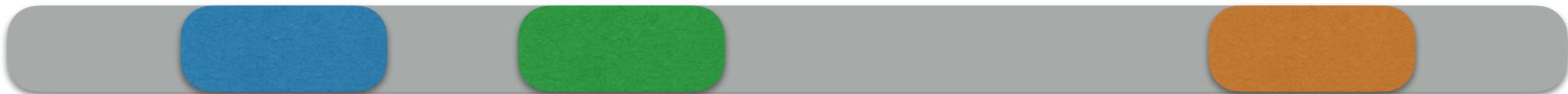


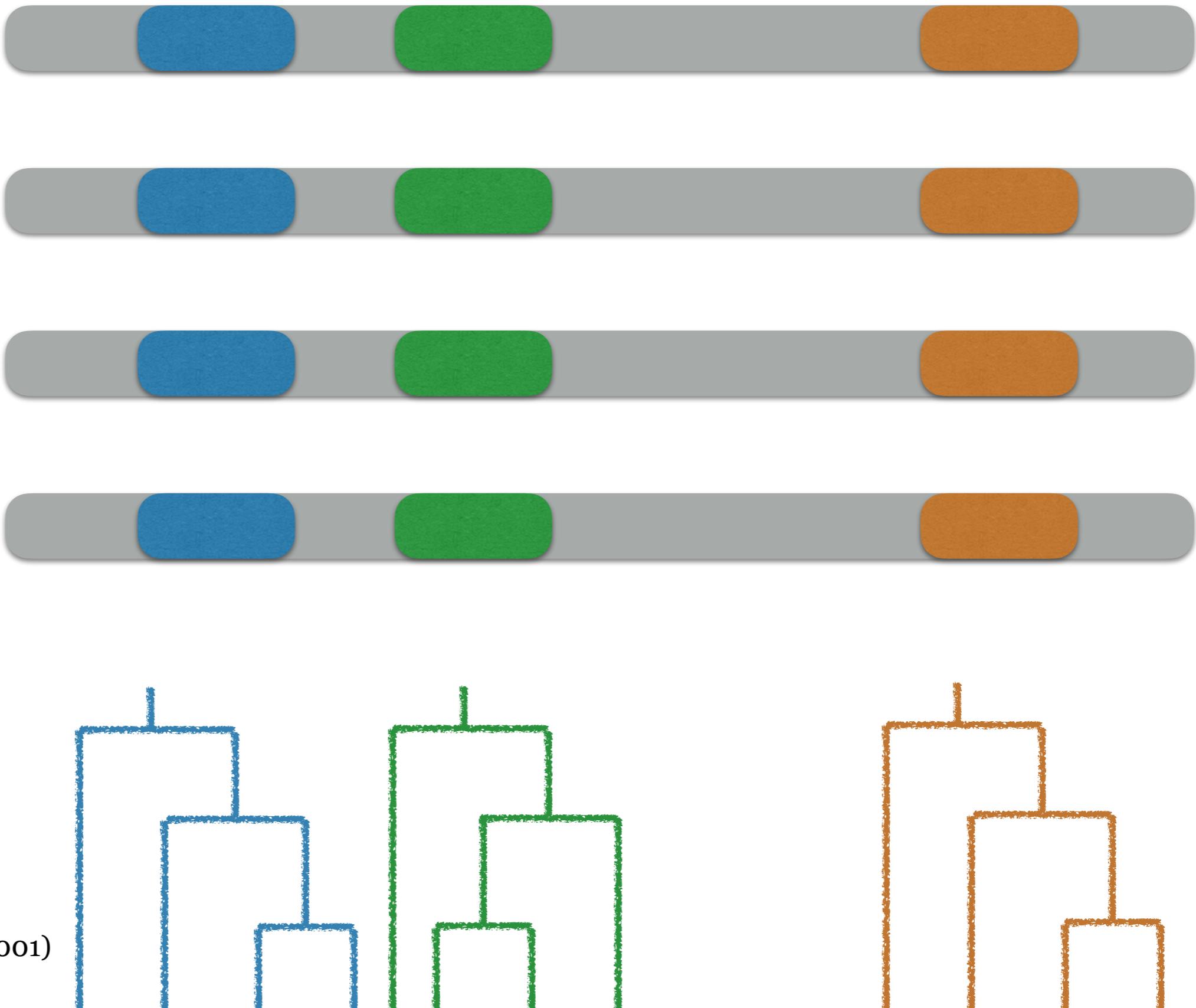
Statistically
inconsistent

(Kubatko, Degnan, 2007)
(Roch, Steel, 2015)

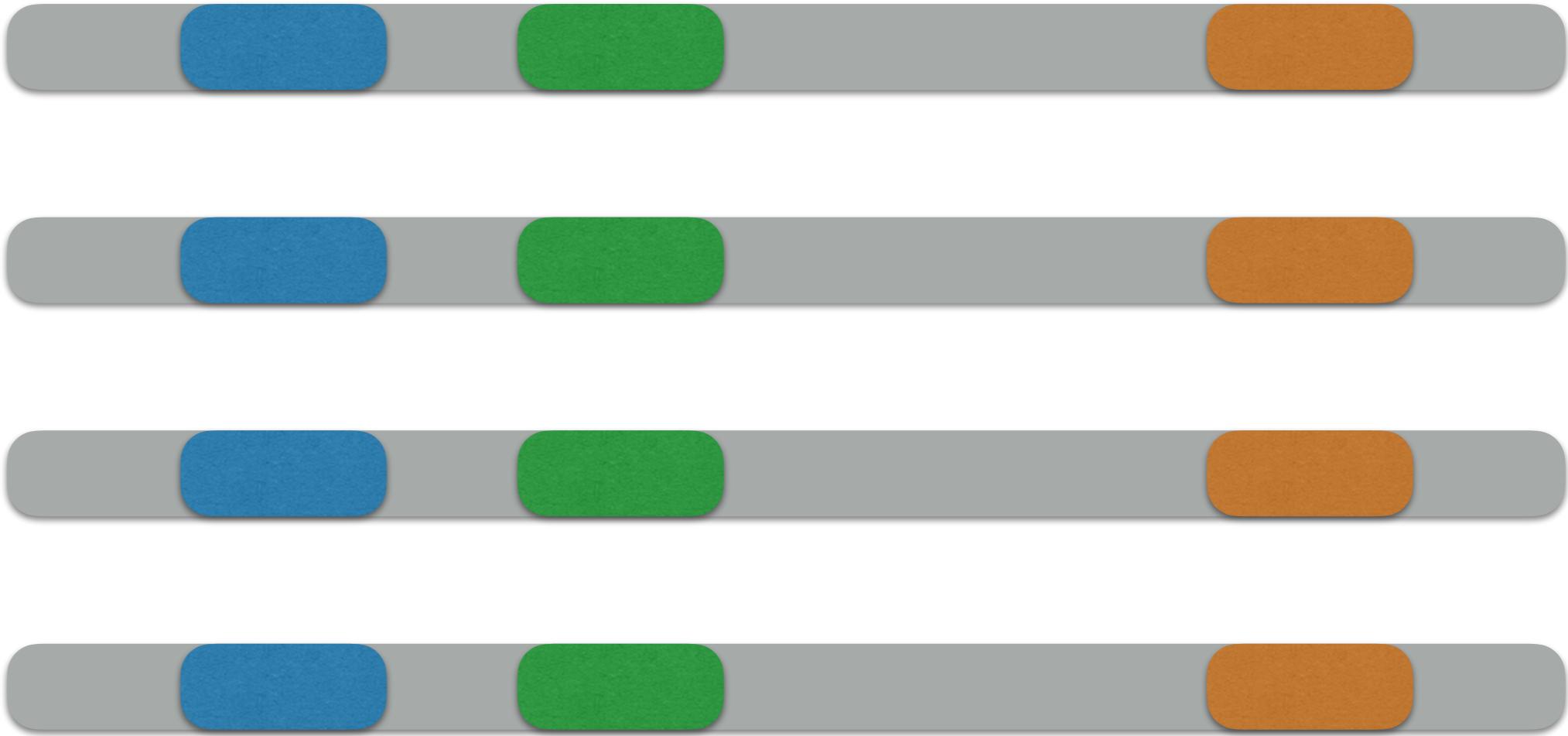


Concatenation or supermatrix



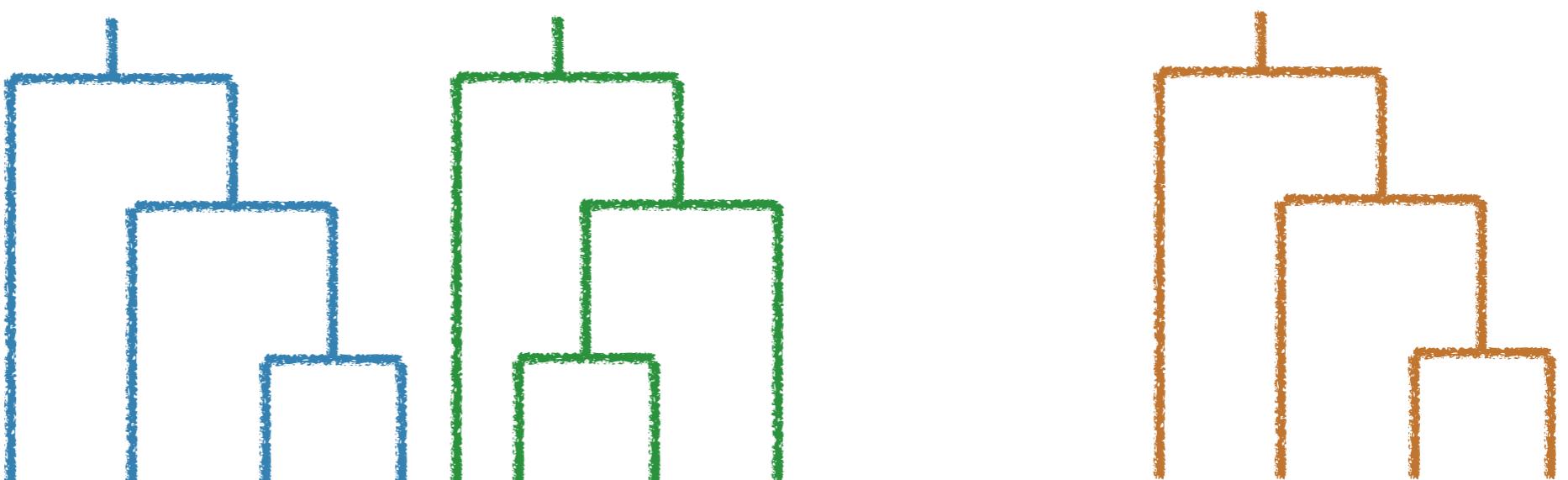


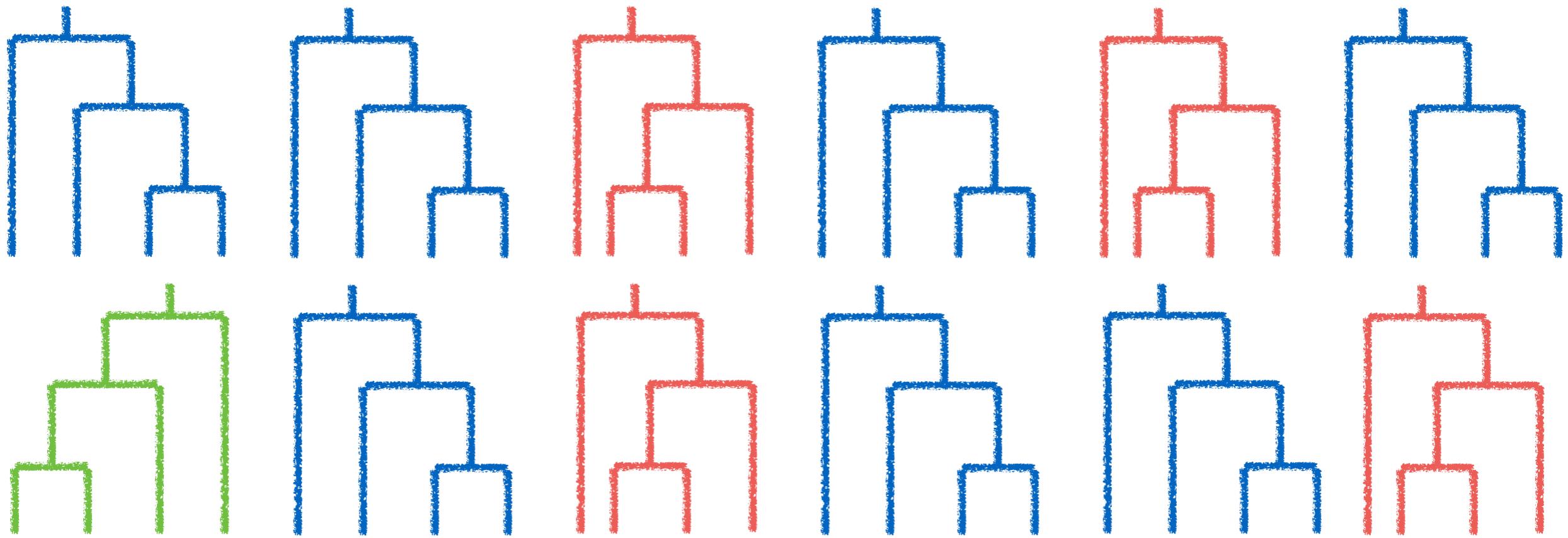
MrBayes
(Huelsenbeck, Ronquist, 2001)
RAXML
(Stamatakis, 2014)
IQ-tree 2
(Minh et al, 2020)



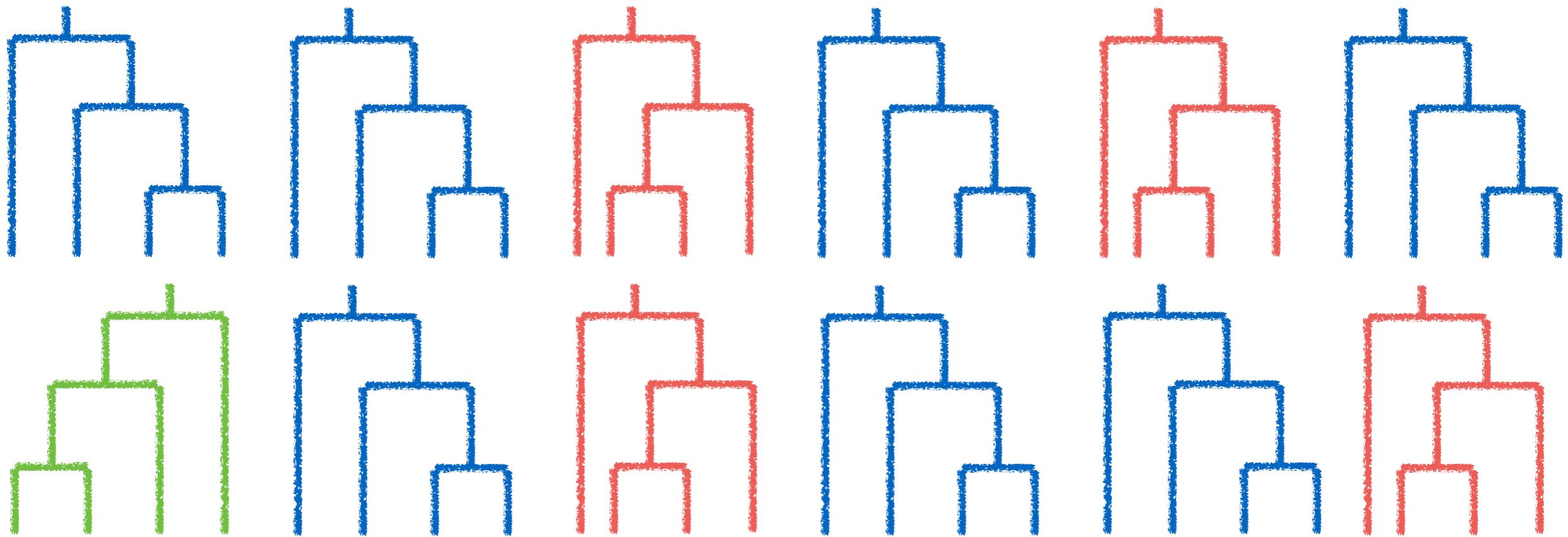
Estimate gene trees

MrBayes
(Huelsenbeck, Ronquist, 2001)
RAxML
(Stamatakis, 2014)
IQ-tree 2
(Minh et al, 2020)



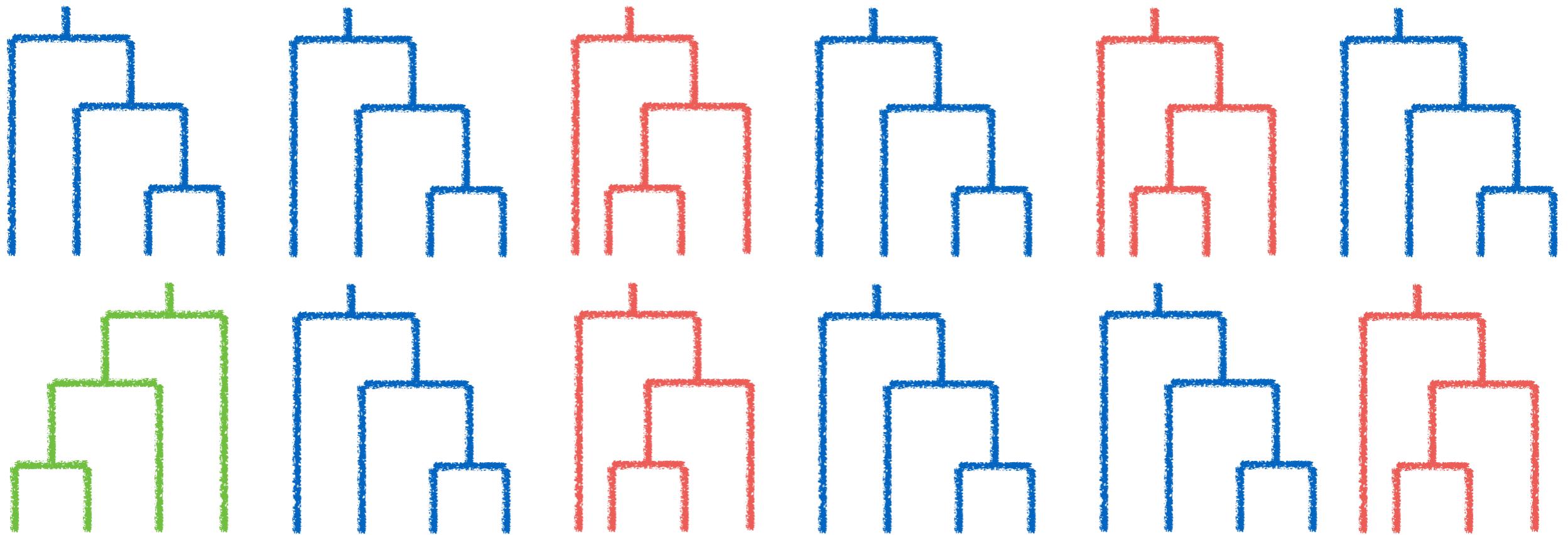


Gene trees



Gene trees

- Estimation error
- Incomplete lineage sorting
- Gene flow

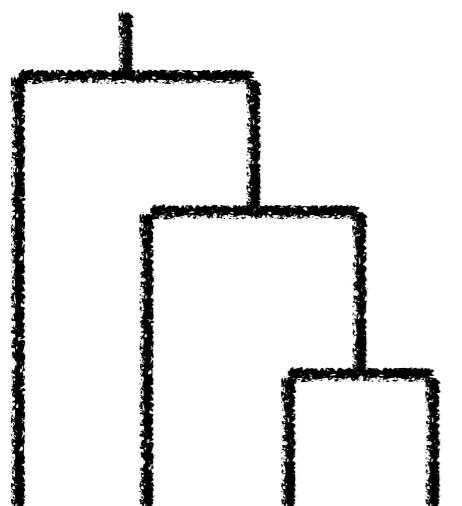
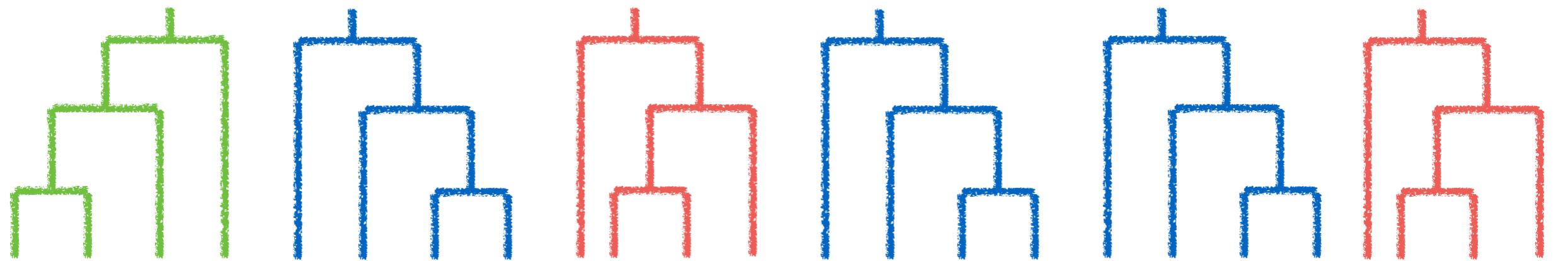
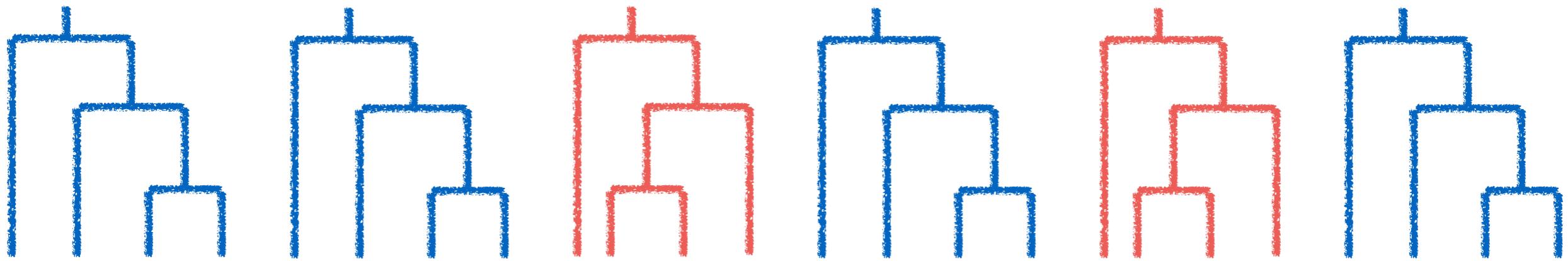


Gene trees

- Estimation error
- Incomplete lineage sorting
- Gene flow



Species evolutionary
history



Gene trees

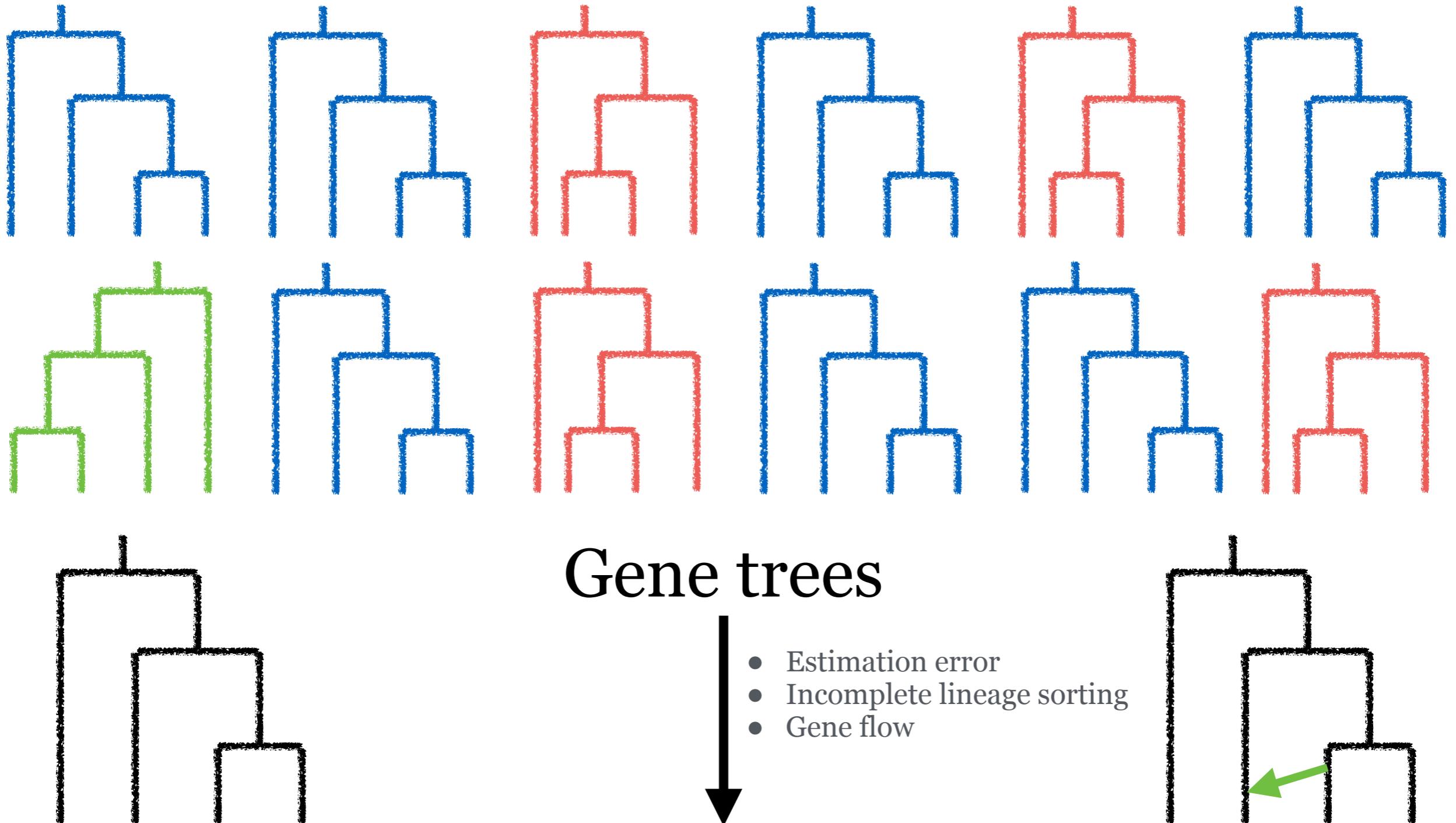


- Estimation error
- Incomplete lineage sorting
- Gene flow

Species evolutionary history

BUCKY (Ané et al, 2007)

ASTRAL (Mirarab et al, 2014)

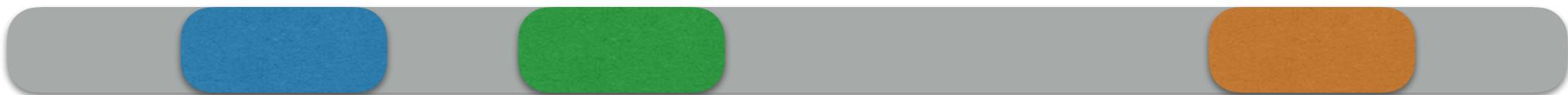


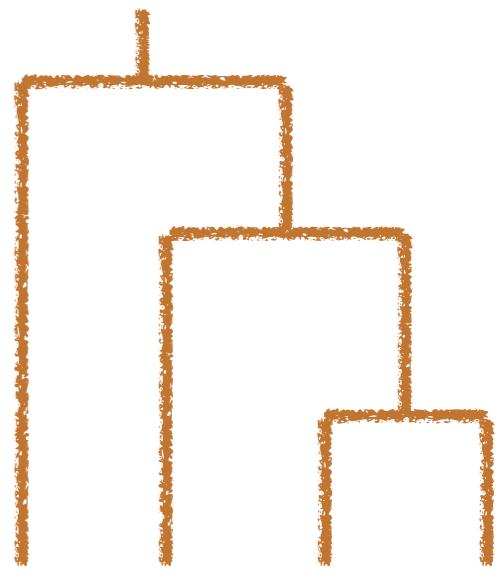
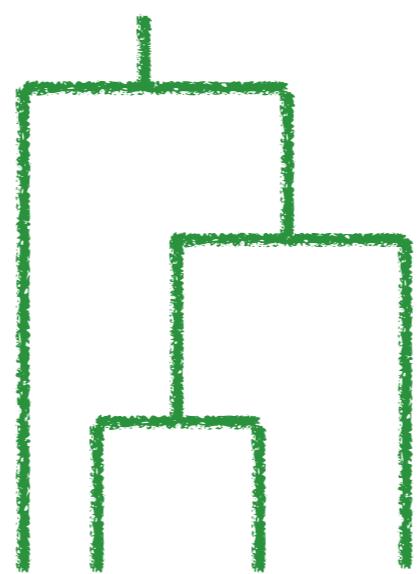
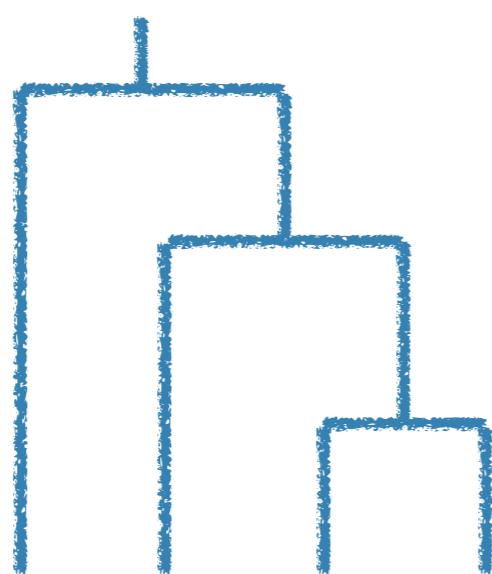
Species evolutionary
history



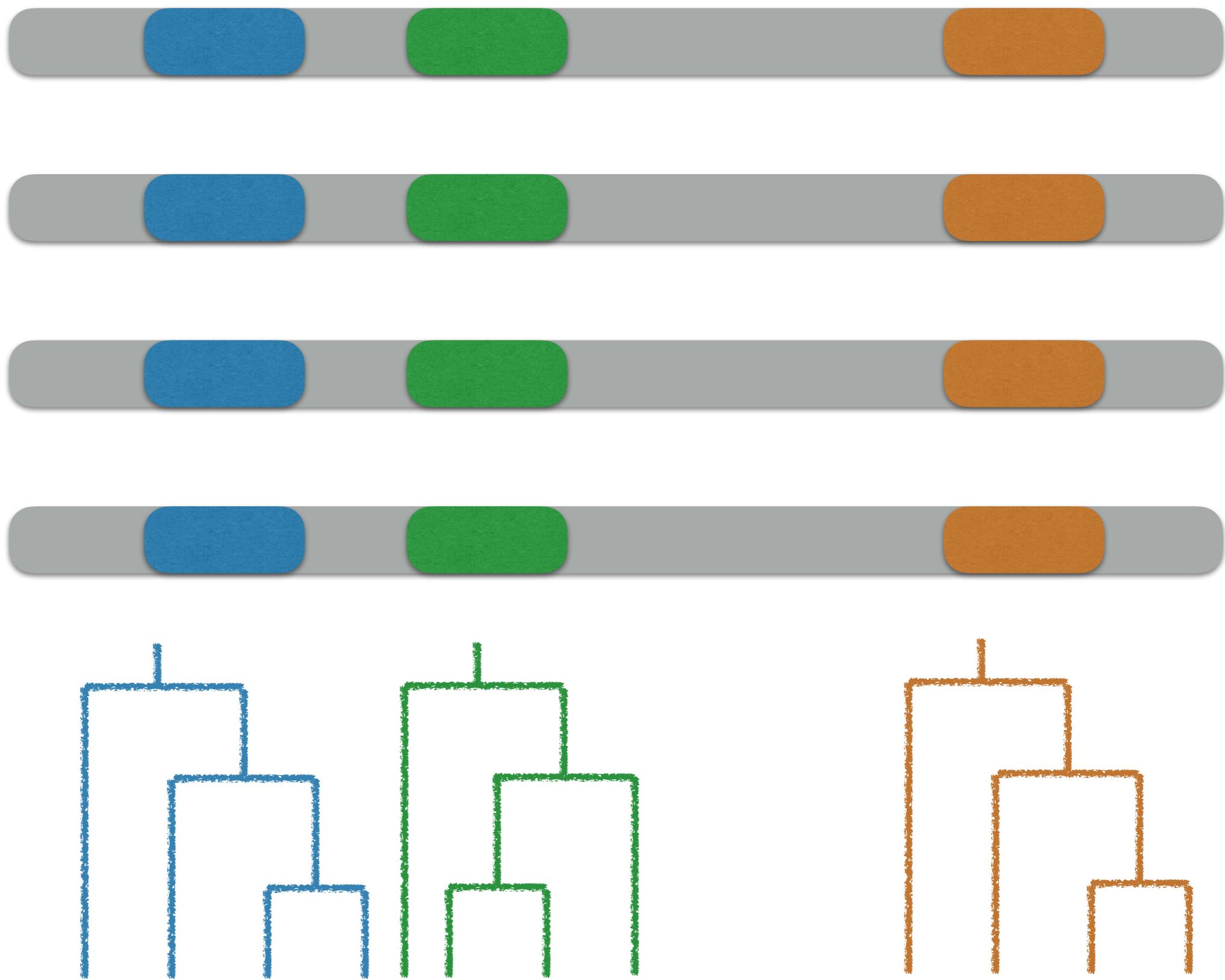
BUCKY (Ané et al, 2007)
ASTRAL (Mirarab et al, 2014)

SNaQ
(Solís-Lemus, Ané, 2016)

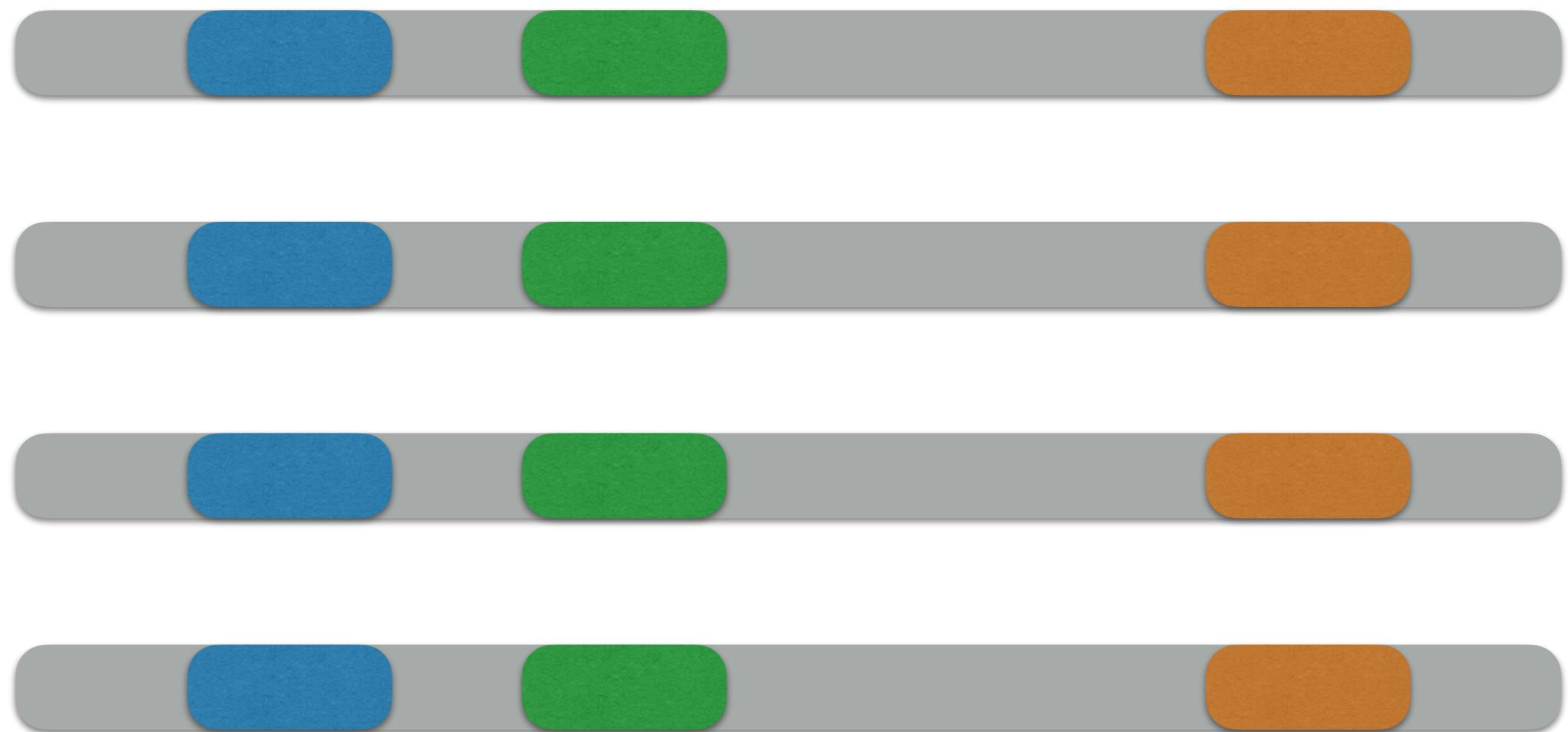




Ortholog
Recombination-free
MDL (Ané, 2011, GBE)



Ortholog
Recombination-free
MDL (Ané, 2011, GBE)

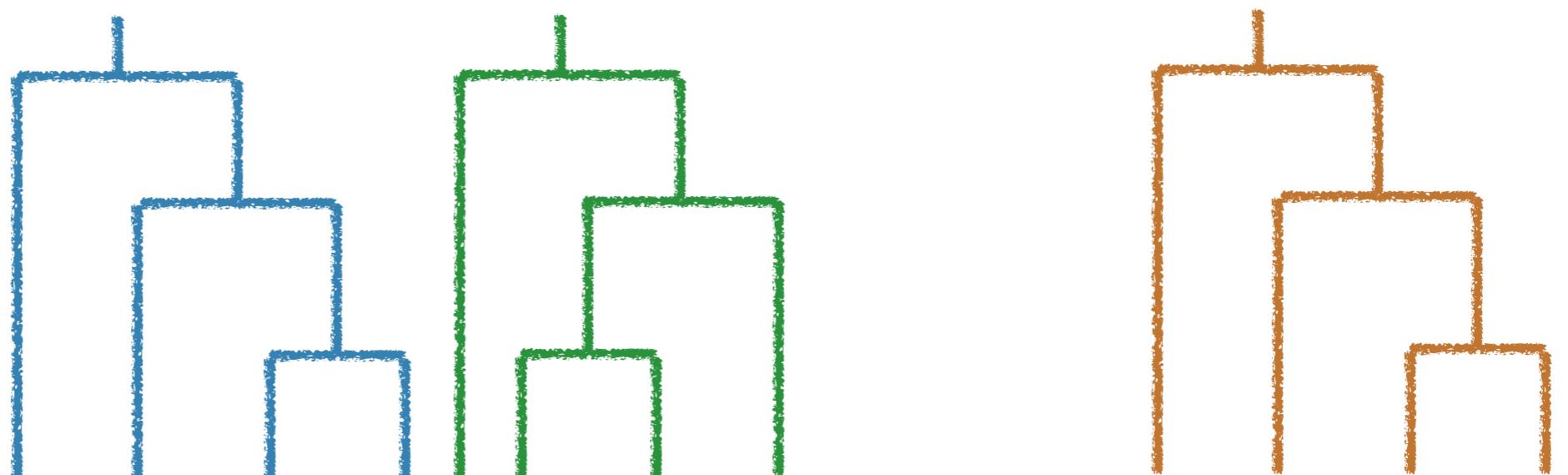


Estimate gene trees

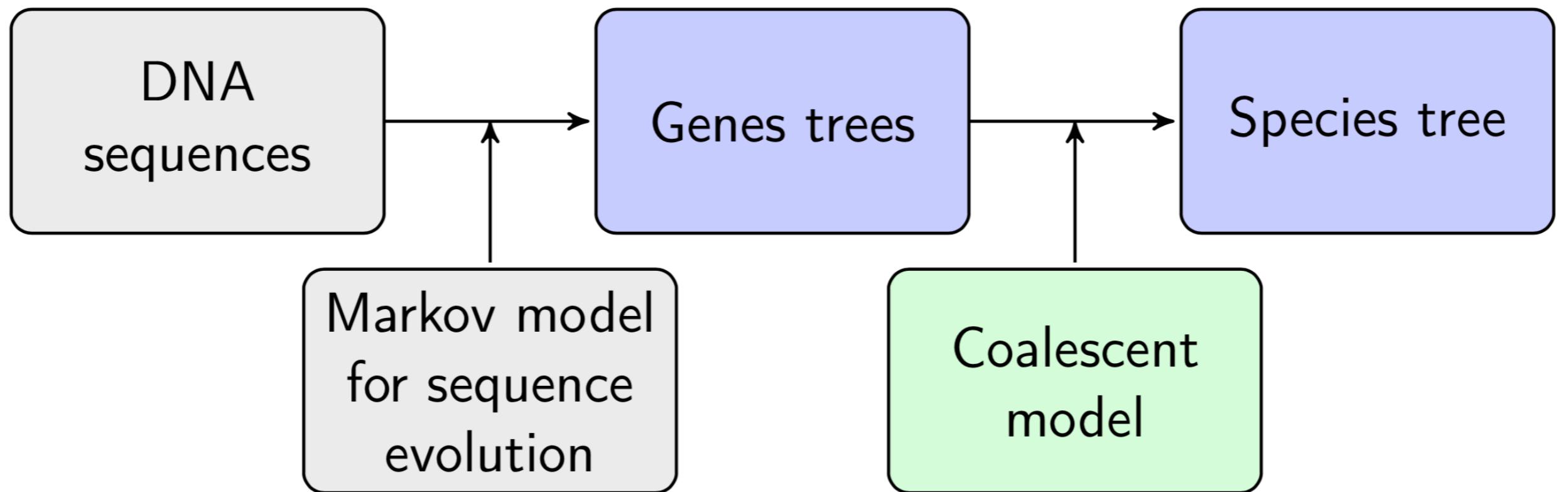
MrBayes
(Huelsenbeck, Ronquist, 2001)

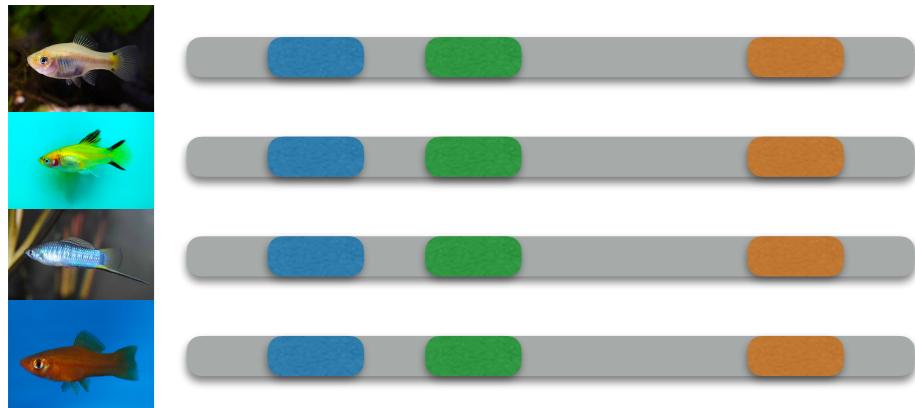
RAXML
(Stamatakis, 2014)

IQ-tree 2
(Minh et al, 2020)

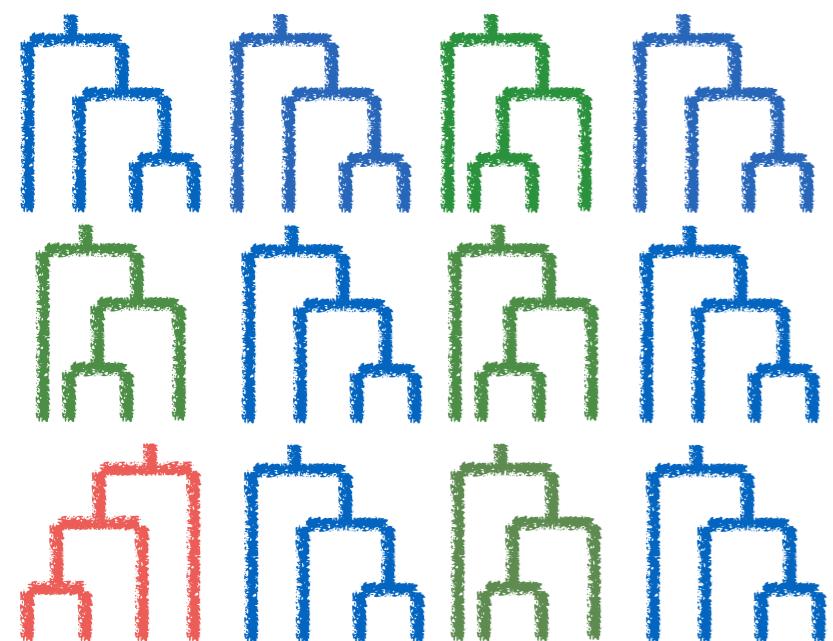


Phylogenetic inference



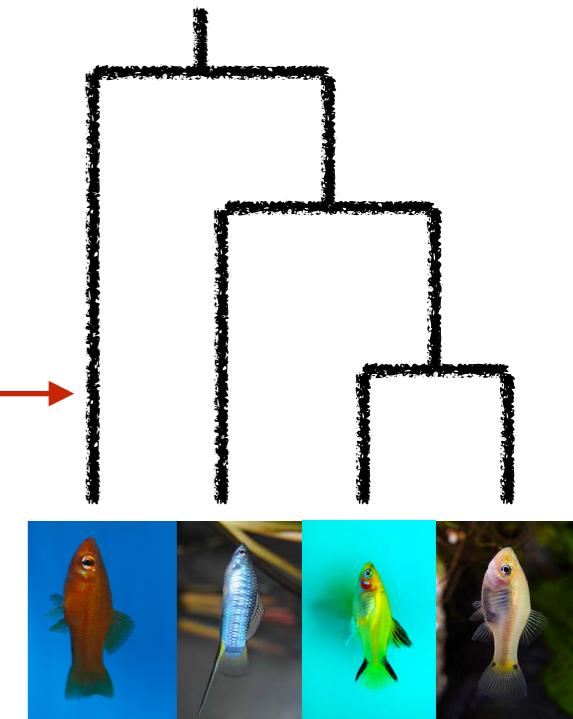


Distances
Parsimony
Likelihood
(Bayesian)

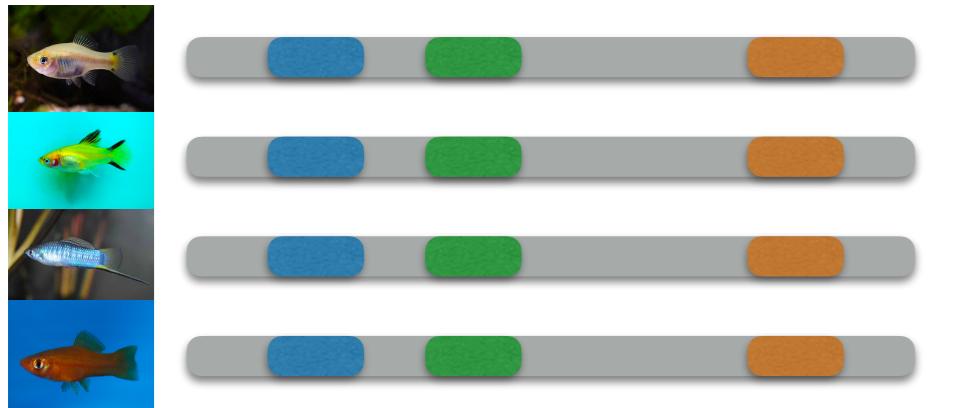


$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

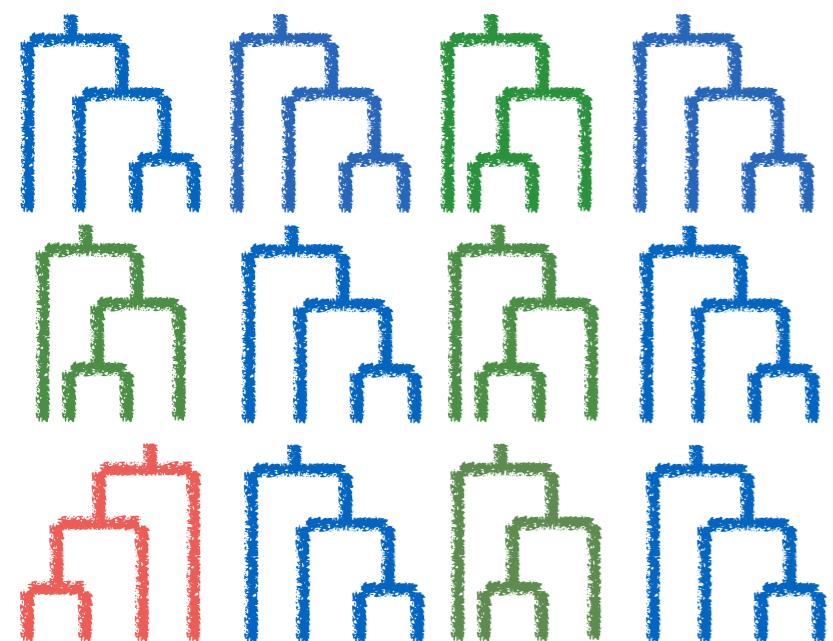
Max. Lik.



Data



Distances
Parsimony
Likelihood
(Bayesian)



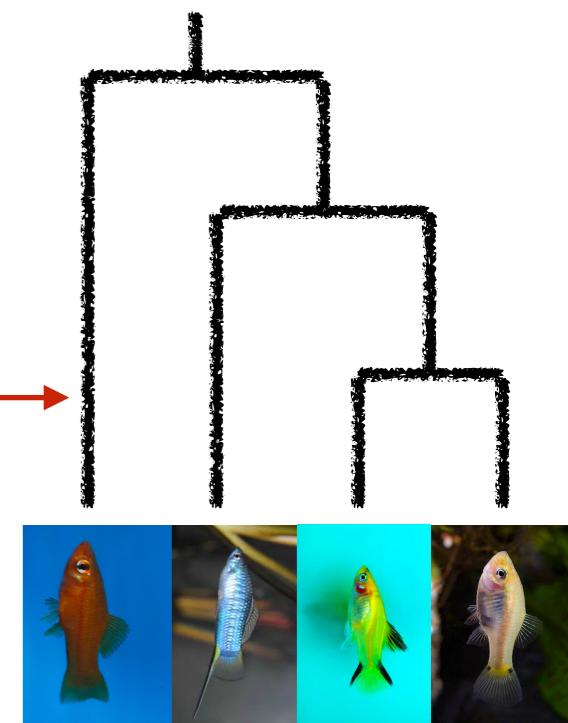
Data



$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

**Multispecies
Coalescent
Model**

Max. Lik.



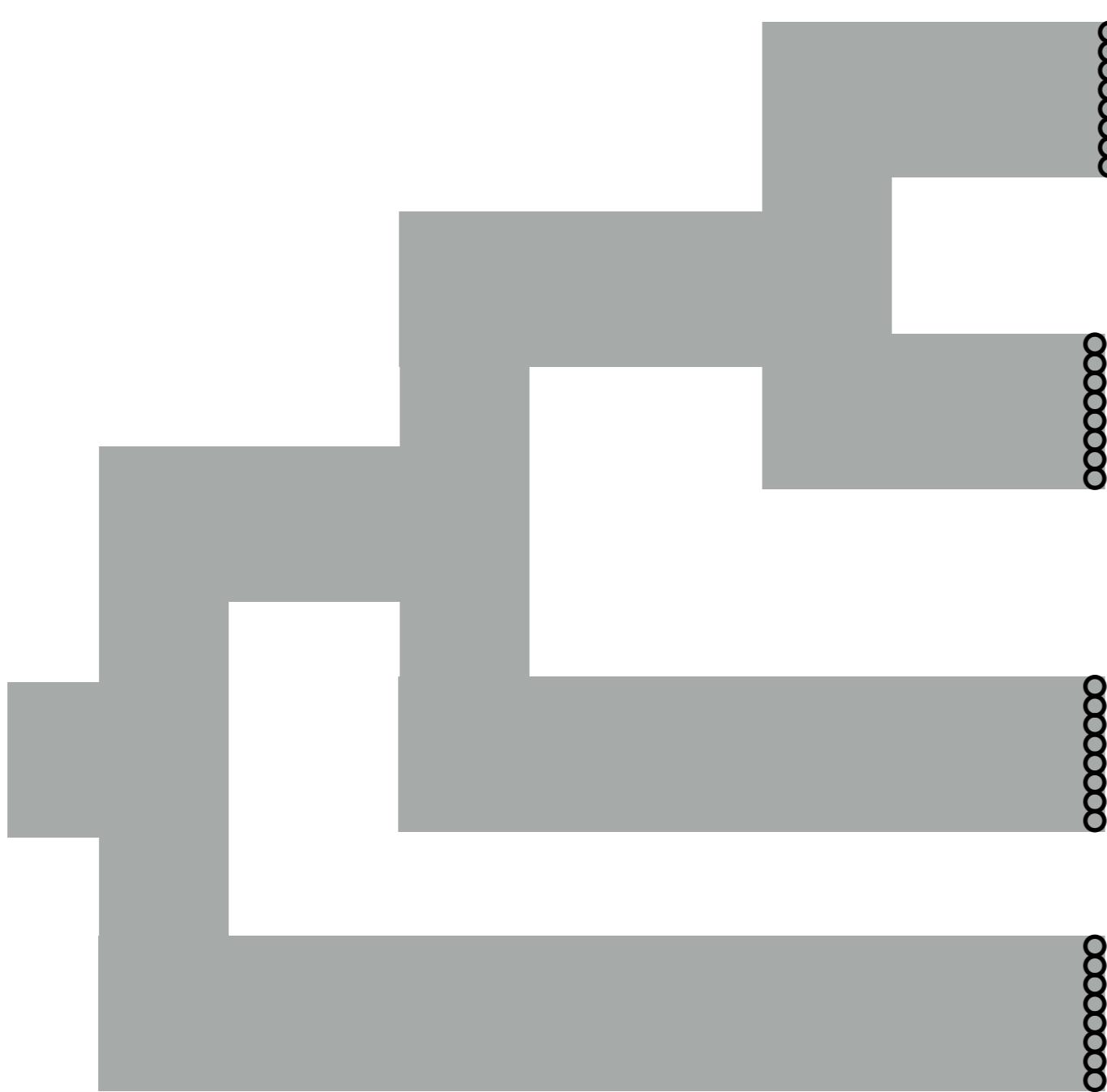
Coalescent model



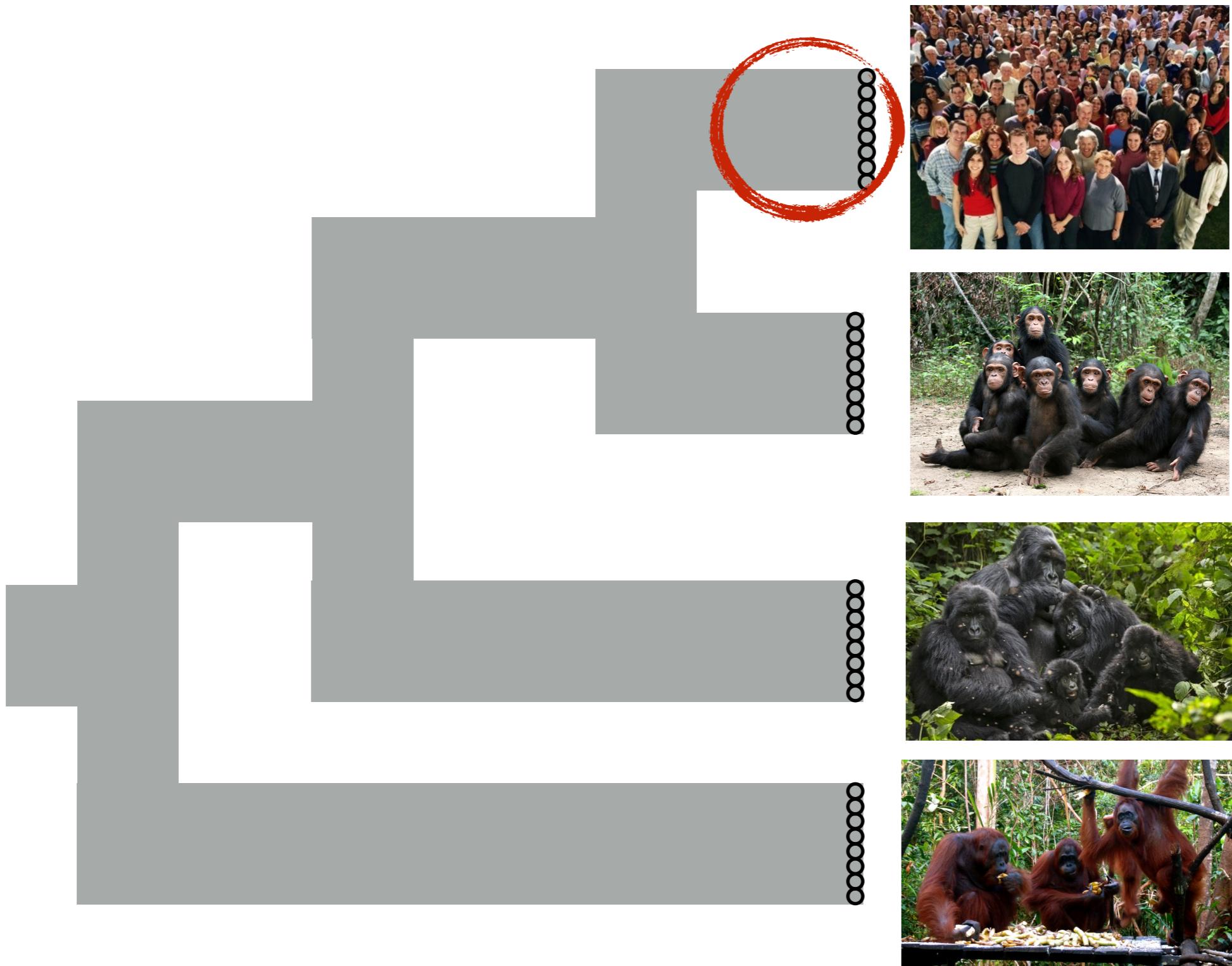
Coalescent model



Coalescent model

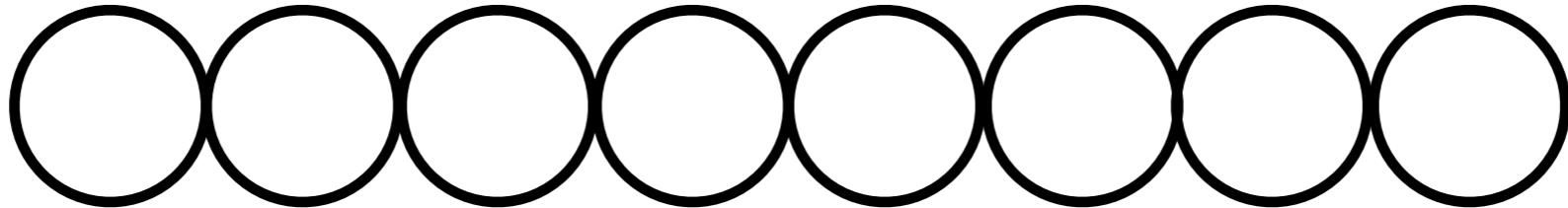


Coalescent model



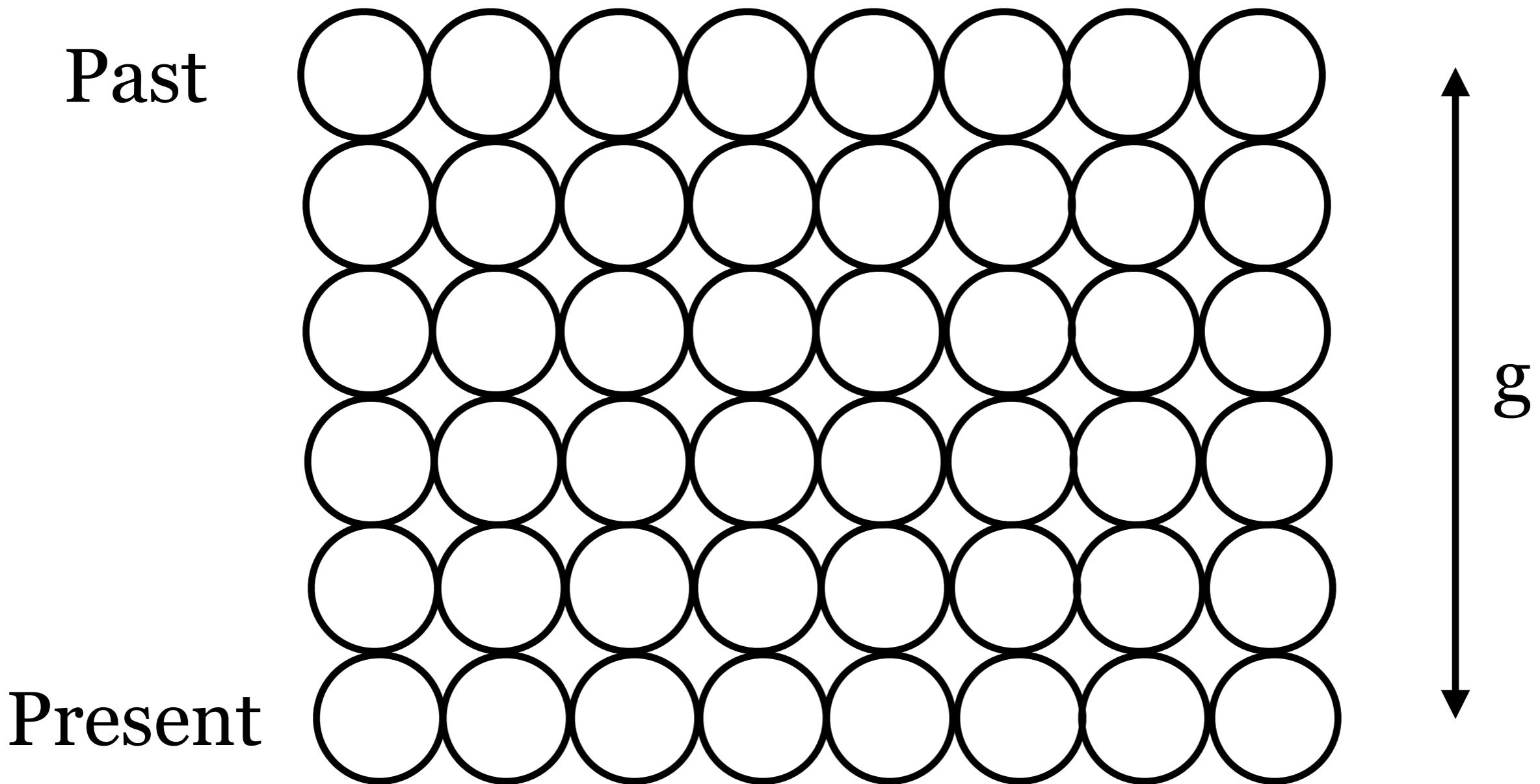
Coalescent model within I population

Present



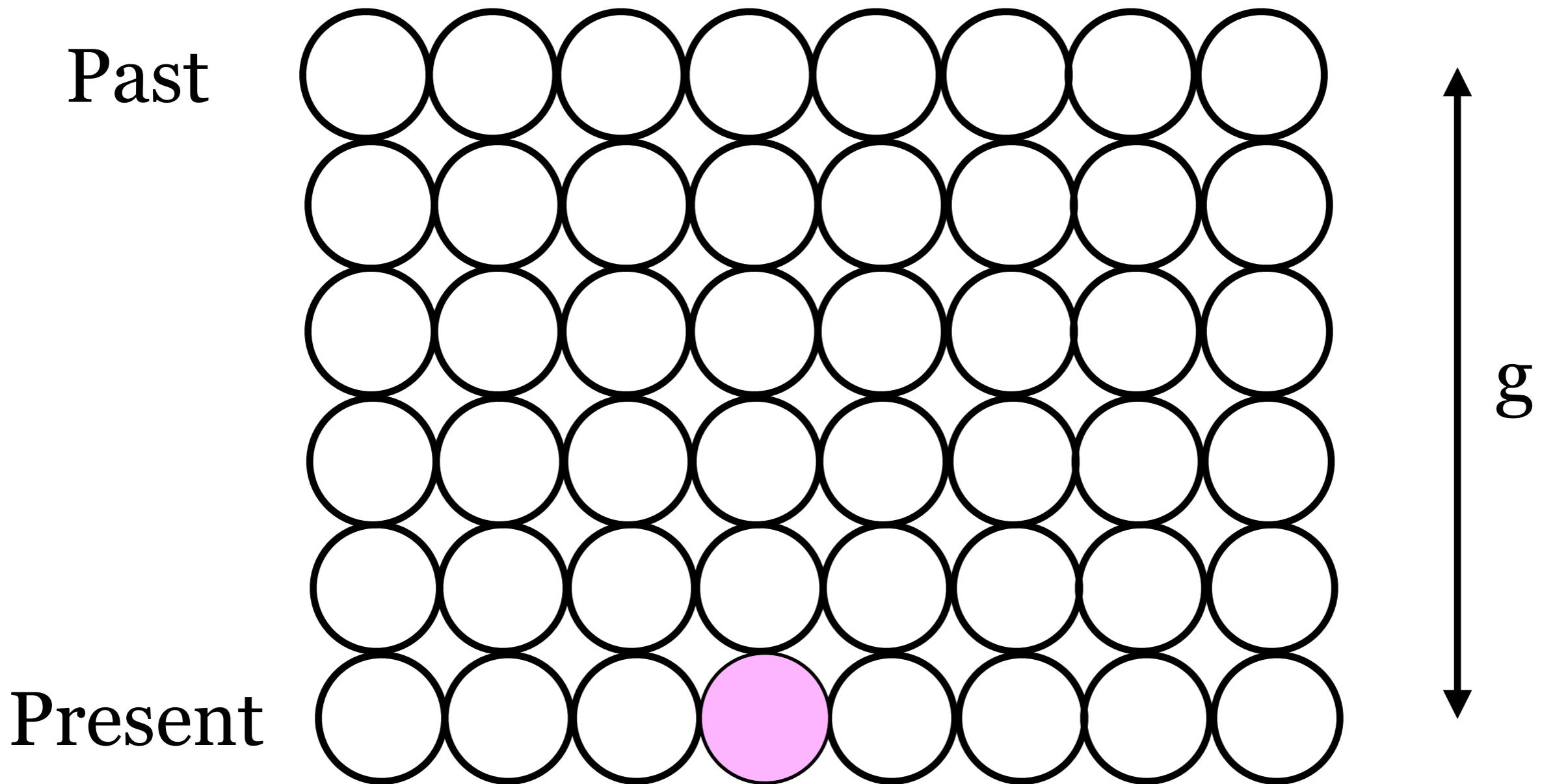
Coalescent model within I

population



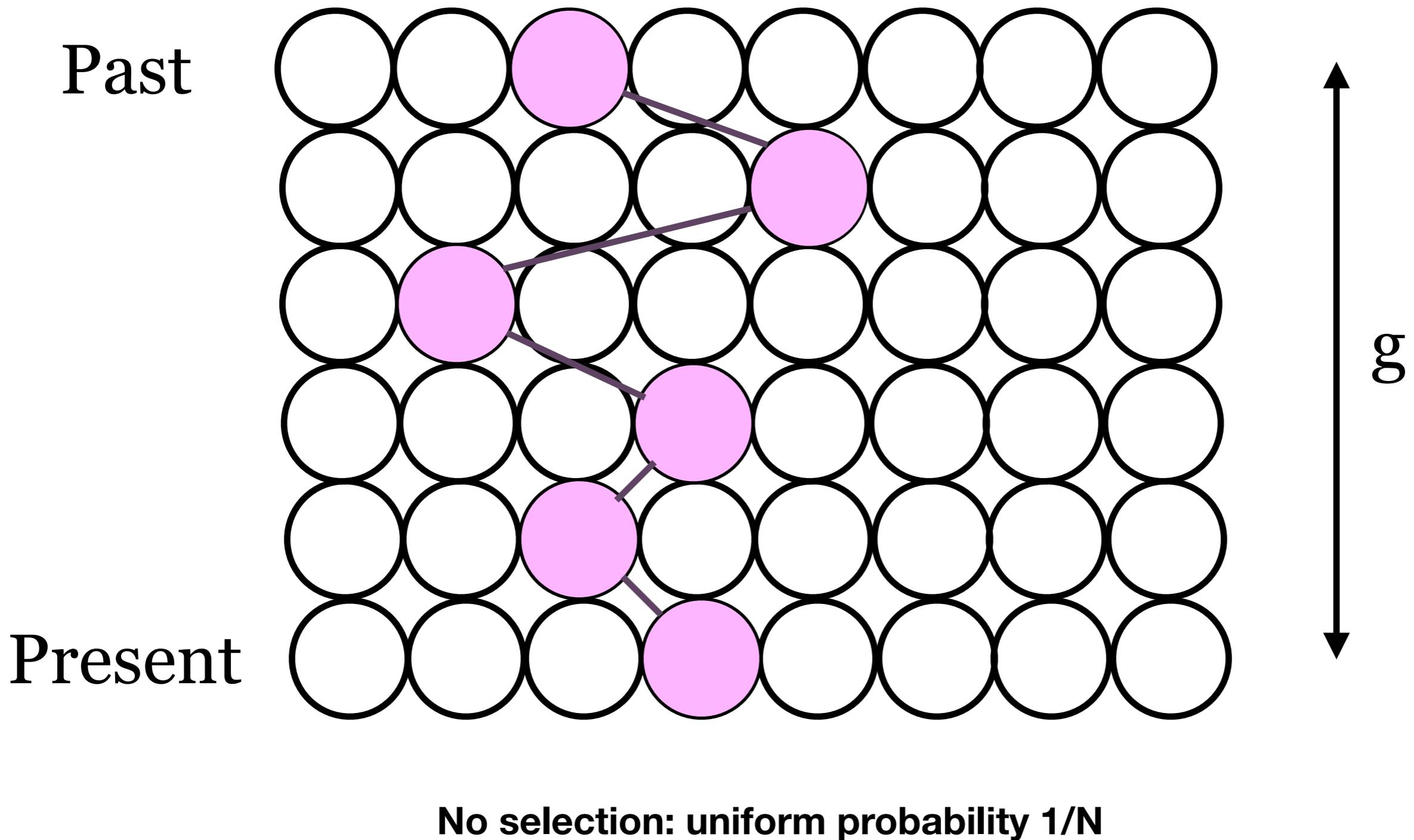
Coalescent model within I

population



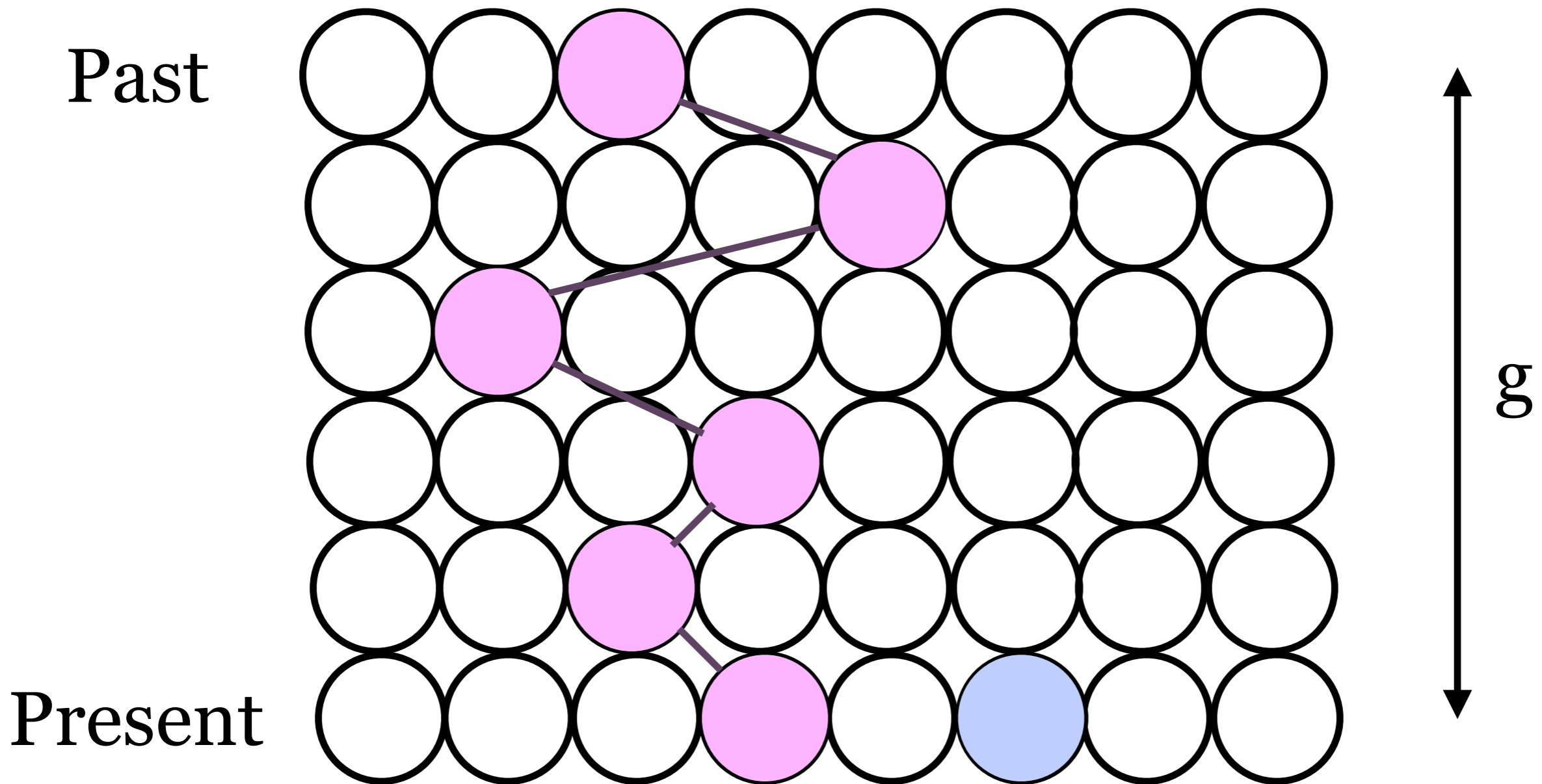
Coalescent model within I

population



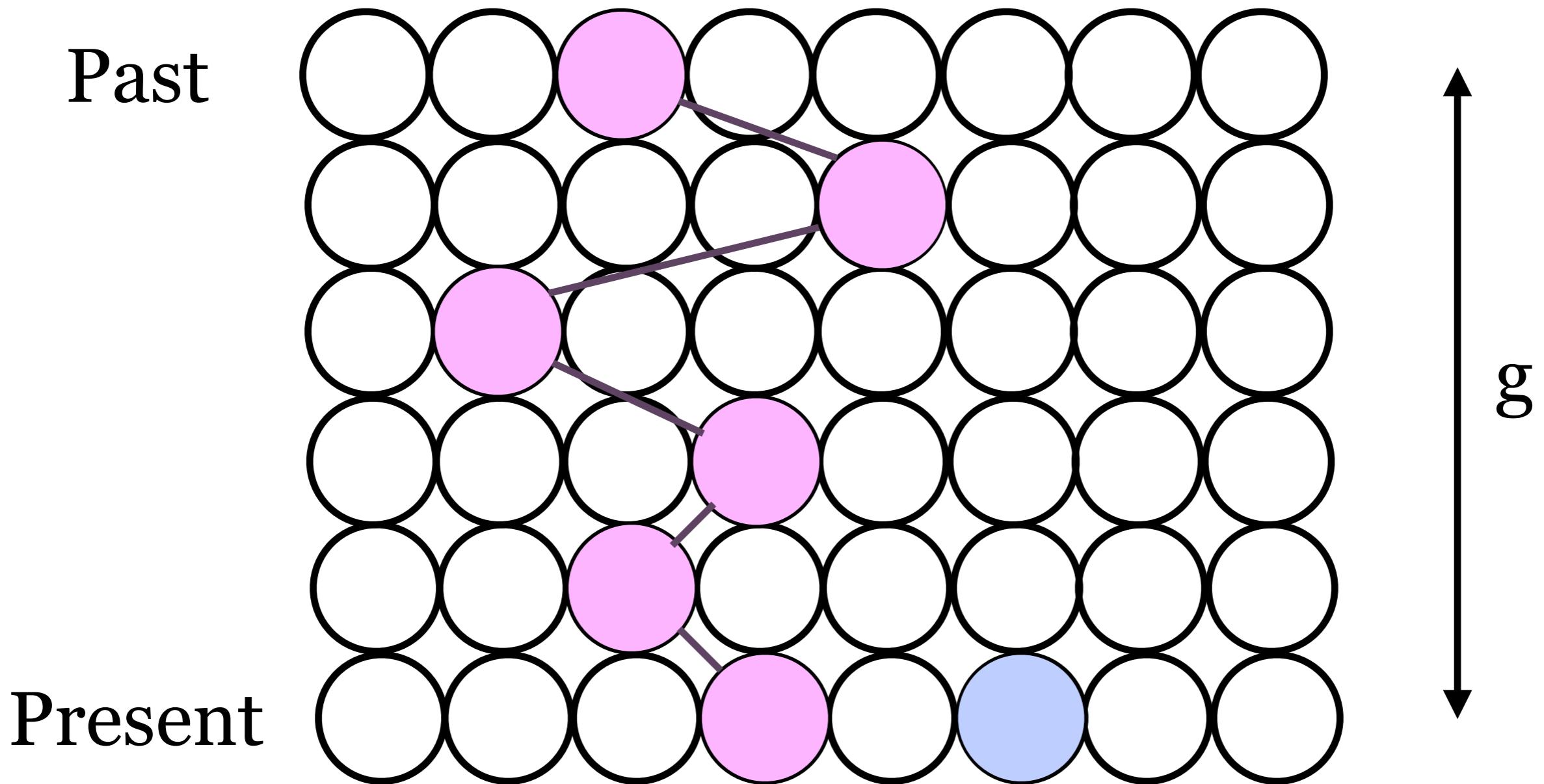
Coalescent model within I

population



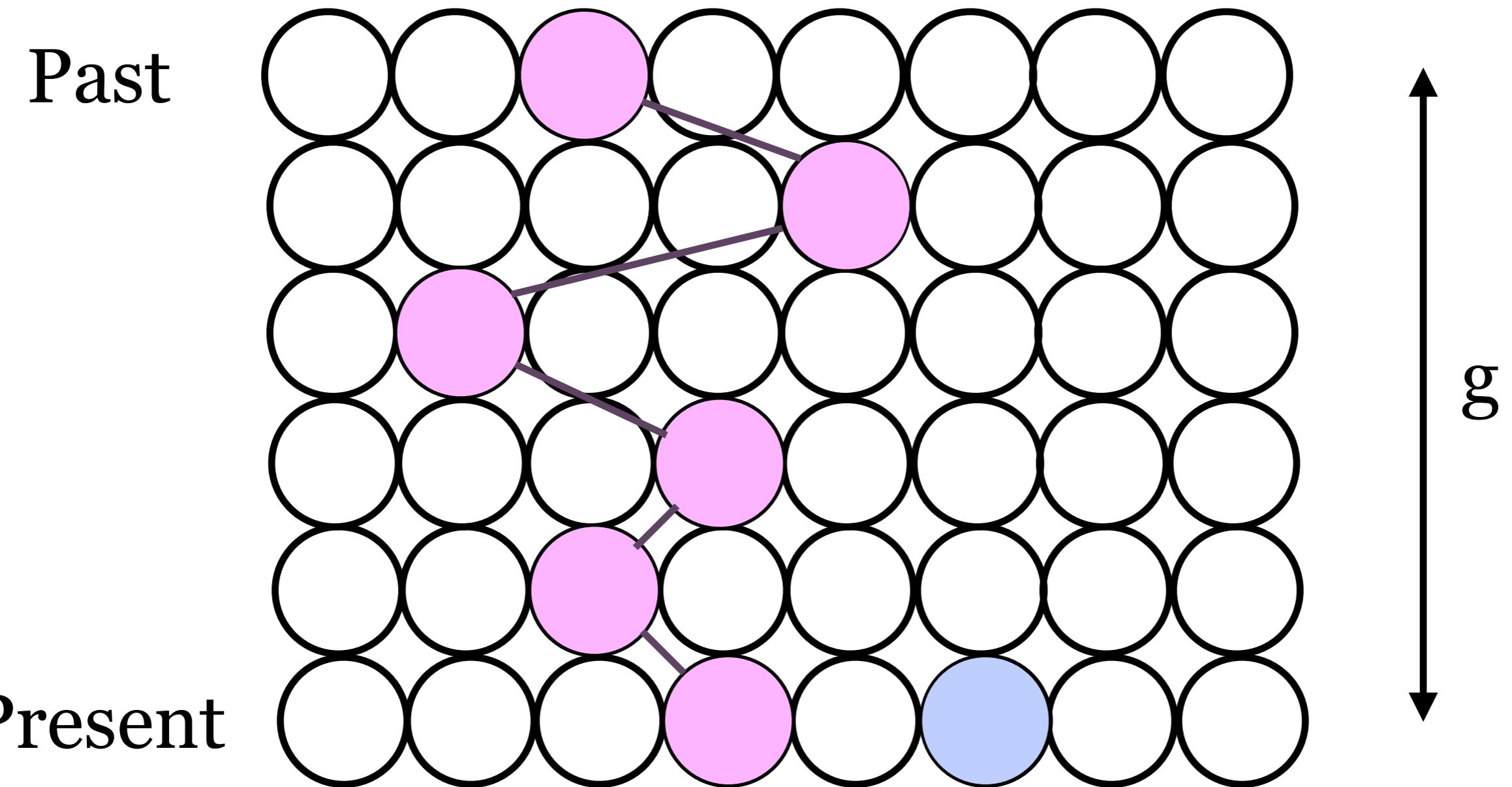
Coalescent model within I

population



How many generations do we have to wait for these two individuals to reach a common ancestor?

Coalescent model within I population

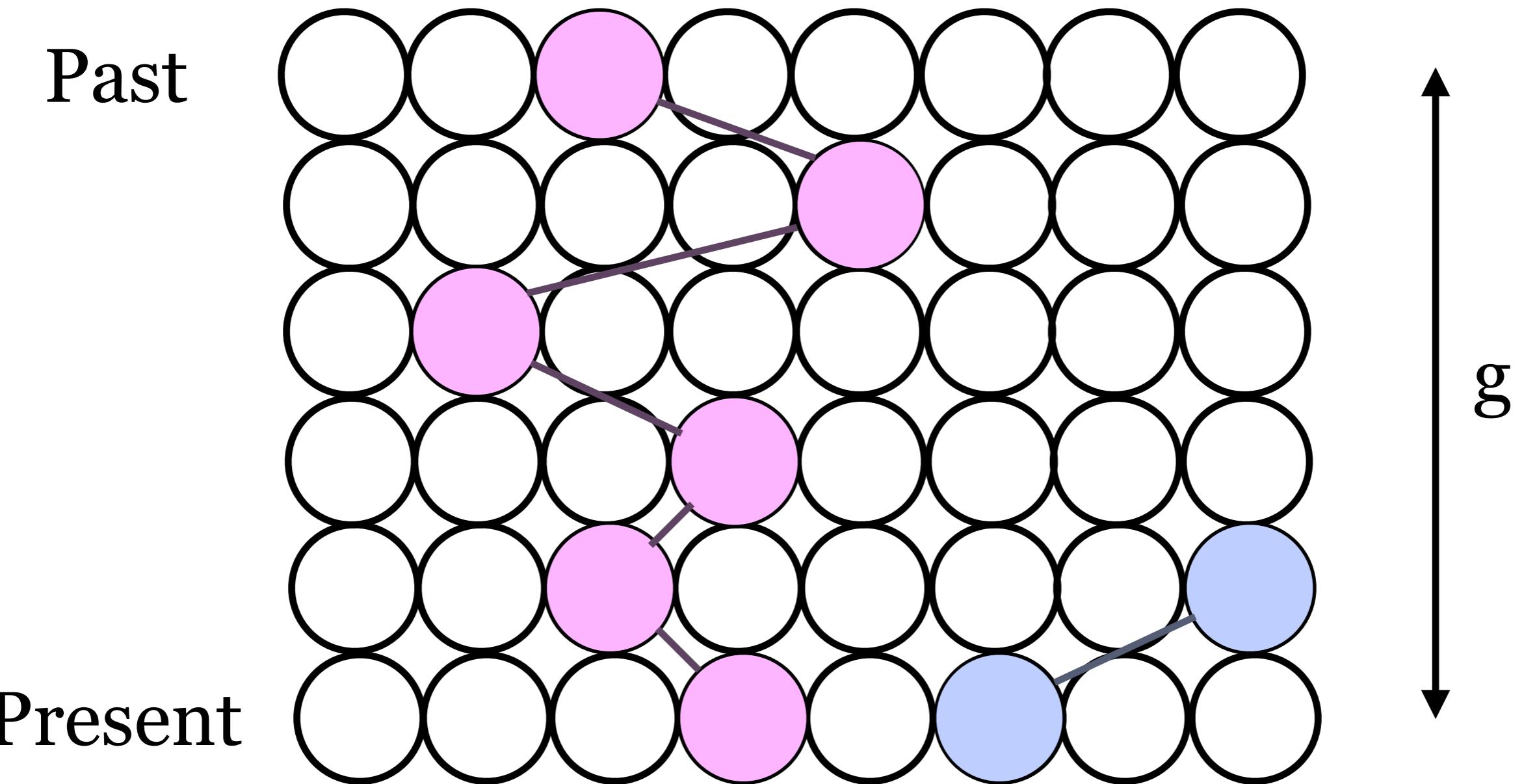


How many generations do we have
to wait for these two individuals to
reach a common ancestor?

$$P(\text{coalesce}) = \frac{1}{N}$$

$$P(\text{no coalesce}) = 1 - \frac{1}{N}$$

Coalescent model within I population



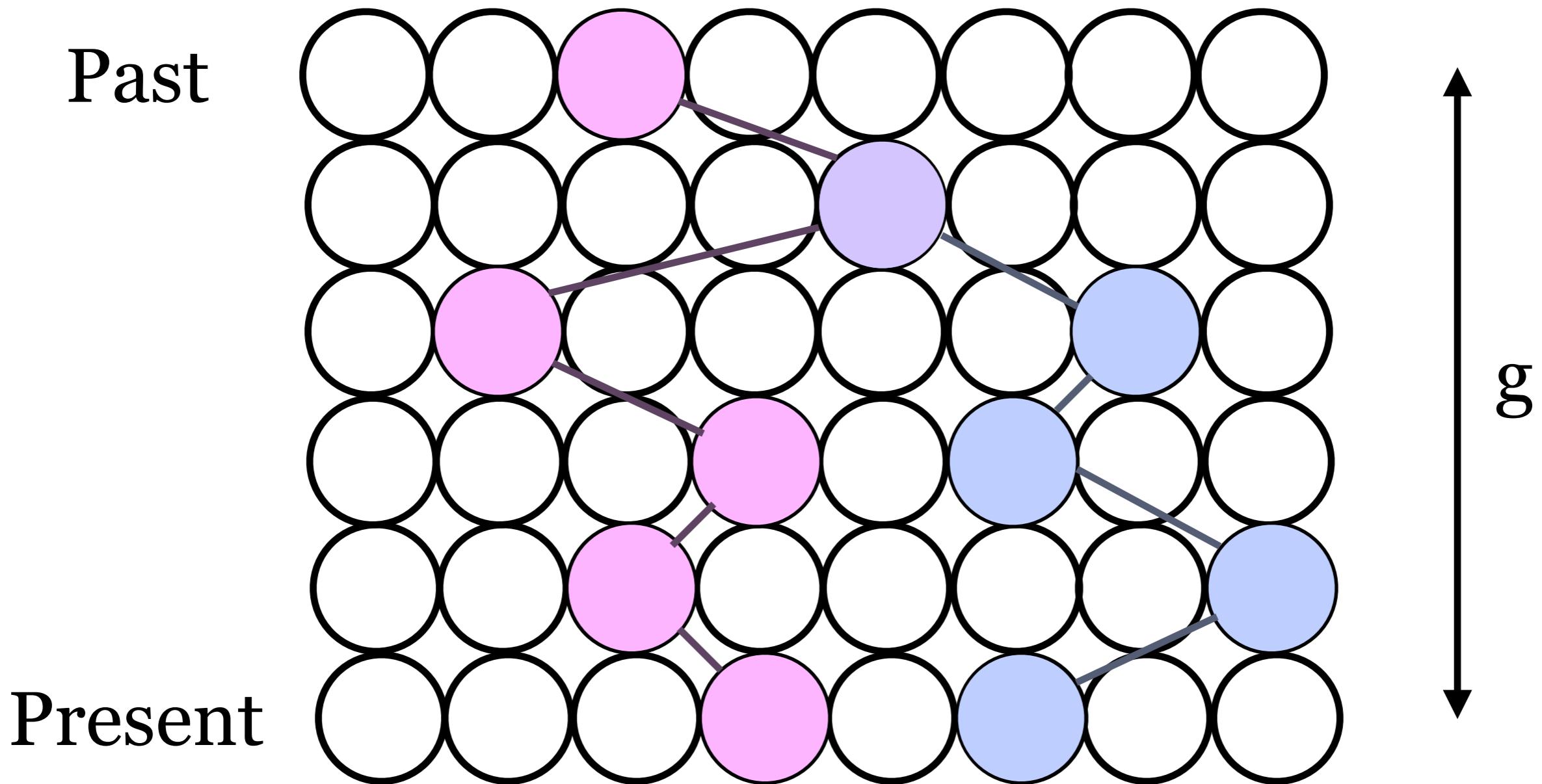
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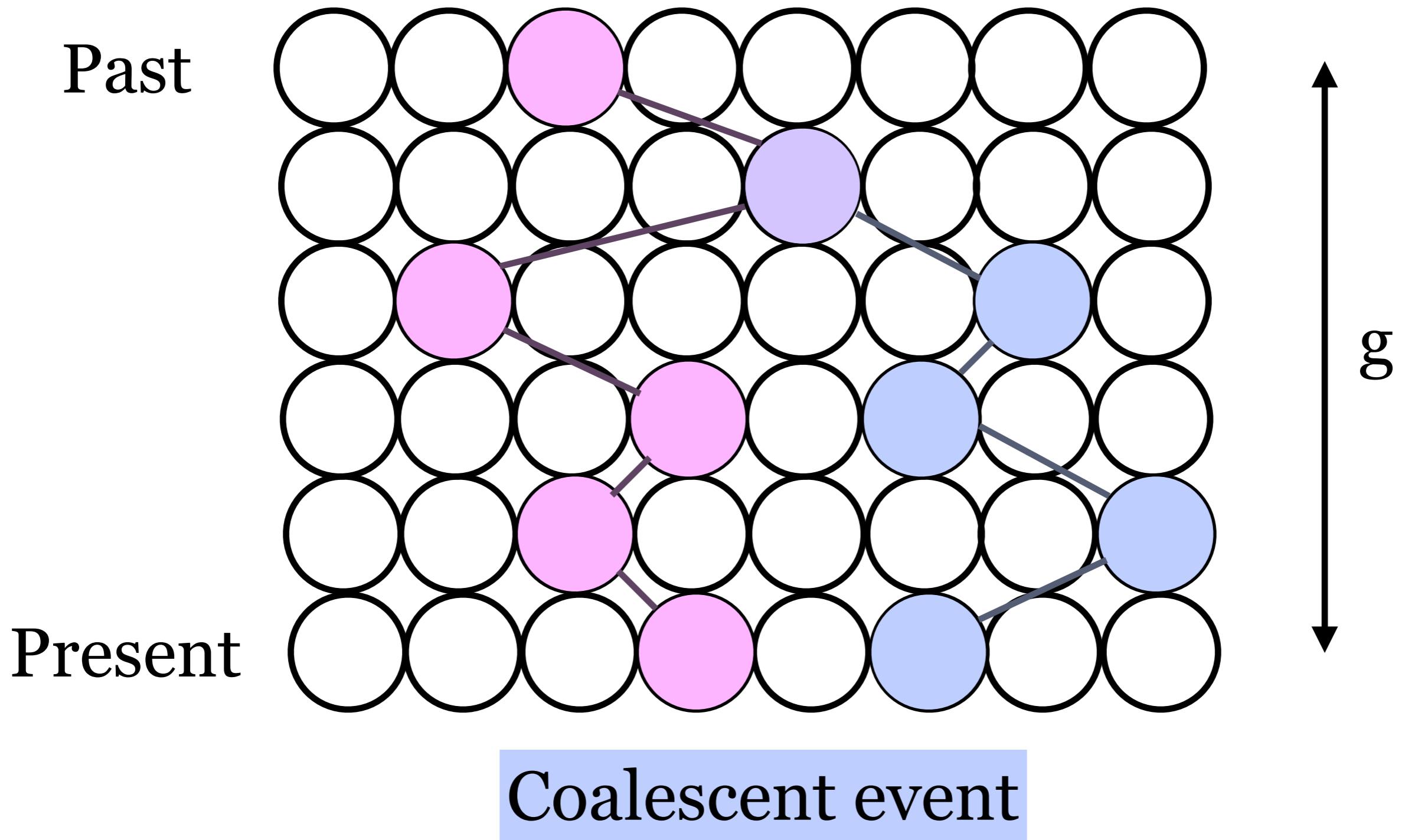
Coalescent model within I

population

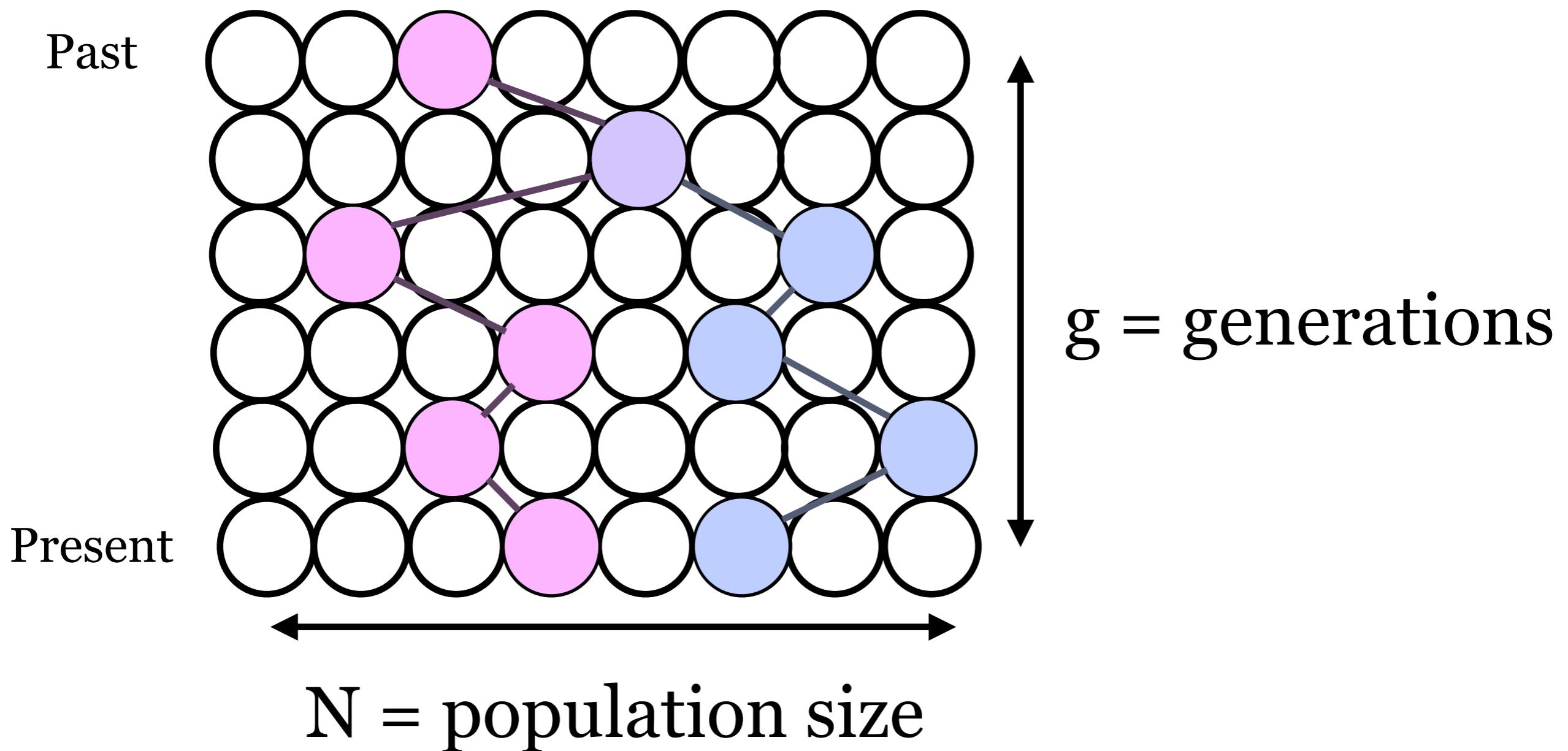


Coalescent model within I

population



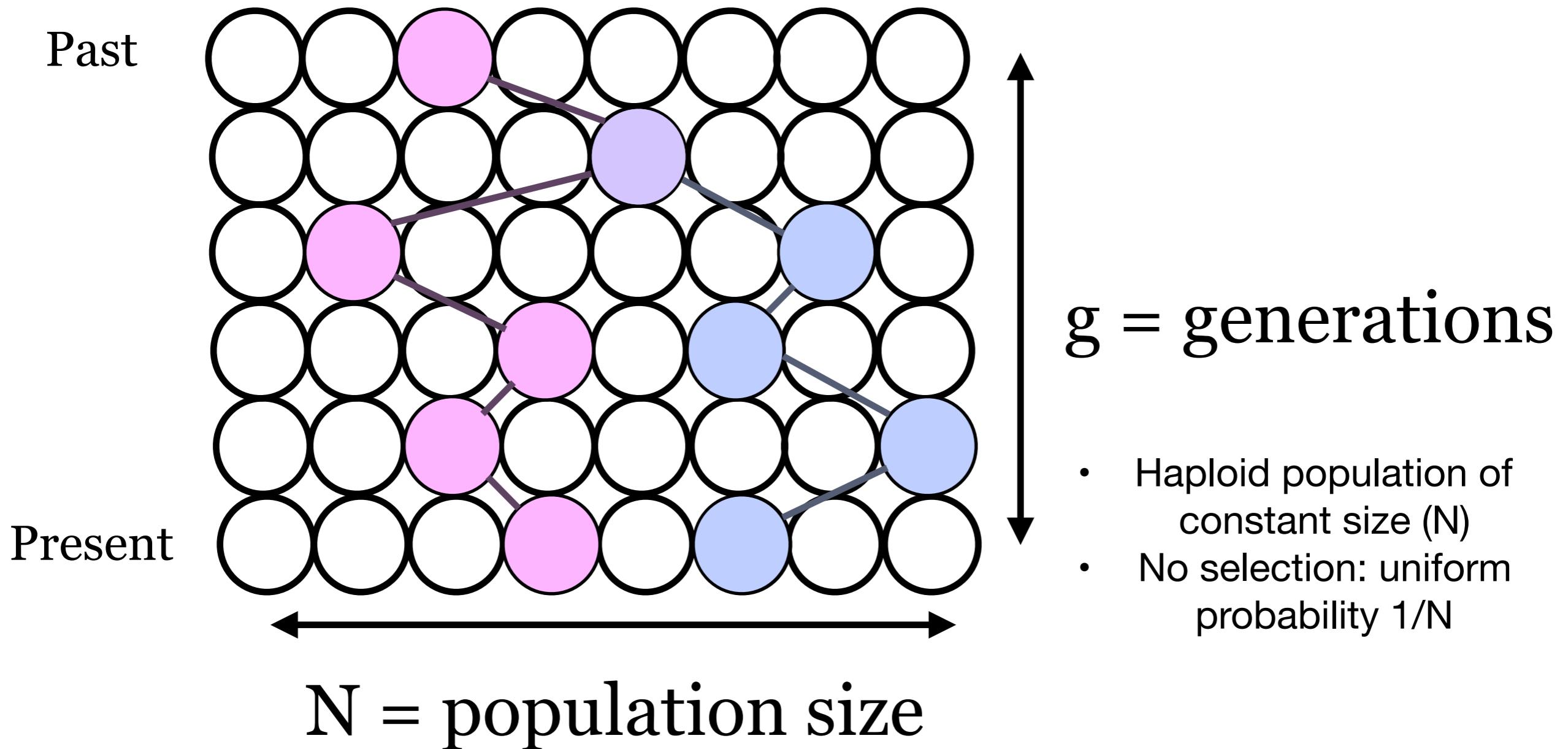
Coalescent model within 1 population



Probability of no coalescence in g generations:

$$\left(1 - \frac{1}{N}\right)^g$$
$$t = g/N \Rightarrow \left(1 - \frac{t}{Nt}\right)^{Nt} \xrightarrow[N \rightarrow \infty]{} e^{-t}$$

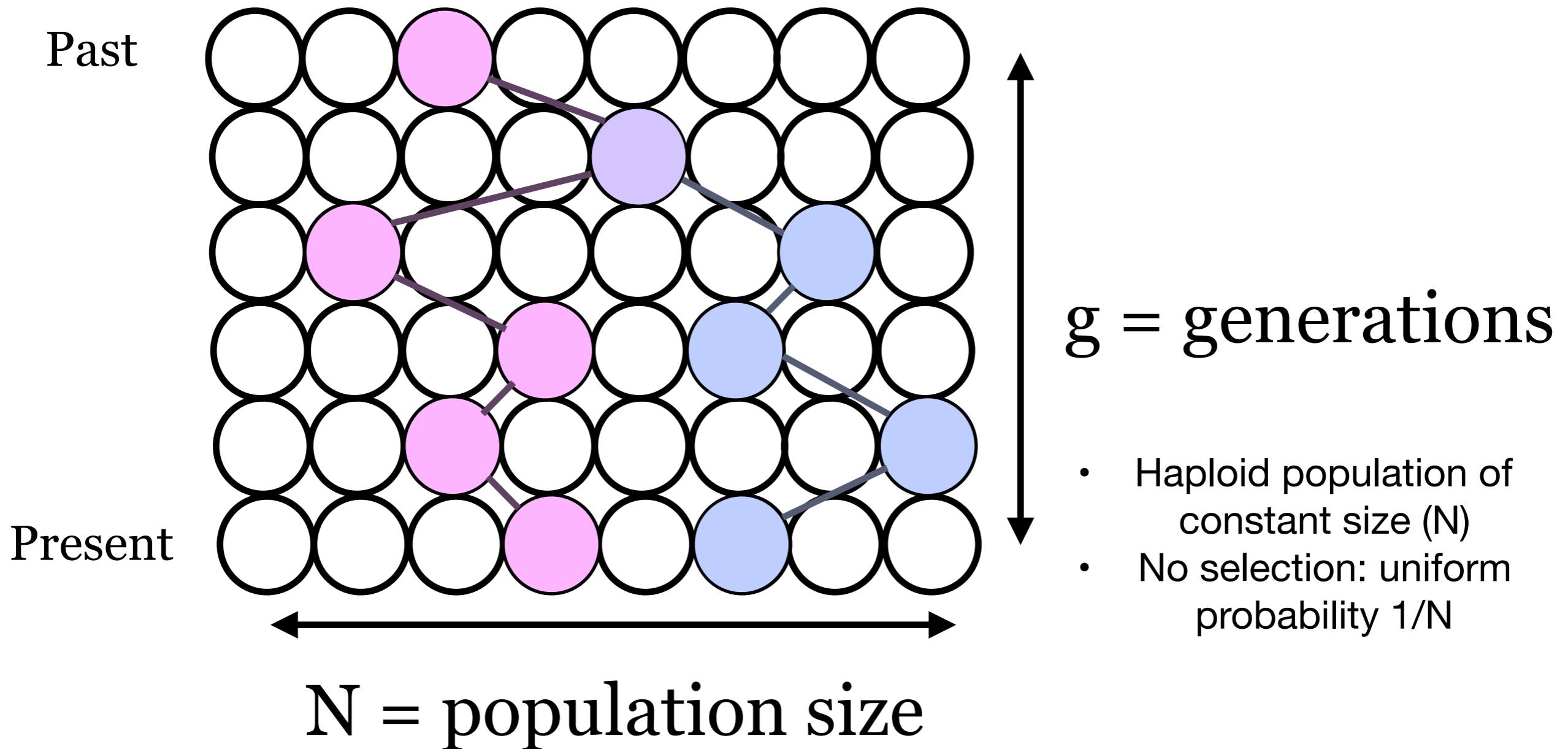
Coalescent model within 1 population



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Coalescent model within 1 population



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Multispecies coalescent on a tree

Probability of no coalescence in g generations: $\left(1 - \frac{1}{N}\right)^g$

$$t = g/N \Rightarrow \left(1 - \frac{t}{Nt}\right)^{Nt} \xrightarrow[N \rightarrow \infty]{} e^{-t}$$

$$T = \frac{g}{N} \text{ coalescent units} \sim \text{Exp}(1)$$

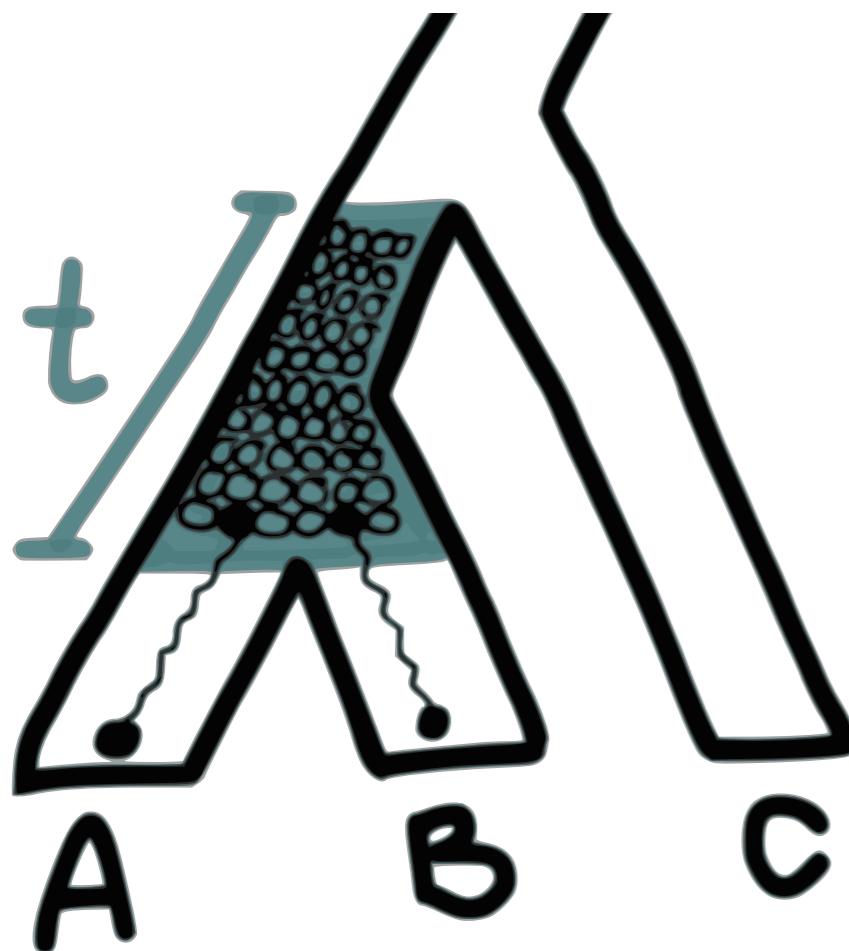
↑
Time to coalesce

$$P(T > t) = e^{-t}$$

Probability of no
coalescence in time t

Multispecies coalescent on a tree

Probability of no coalescence in g generations: $\left(1 - \frac{1}{N}\right)^g$

$$t = g/N \Rightarrow \left(1 - \frac{t}{Nt}\right)^{Nt} \xrightarrow[N \rightarrow \infty]{} e^{-t}$$


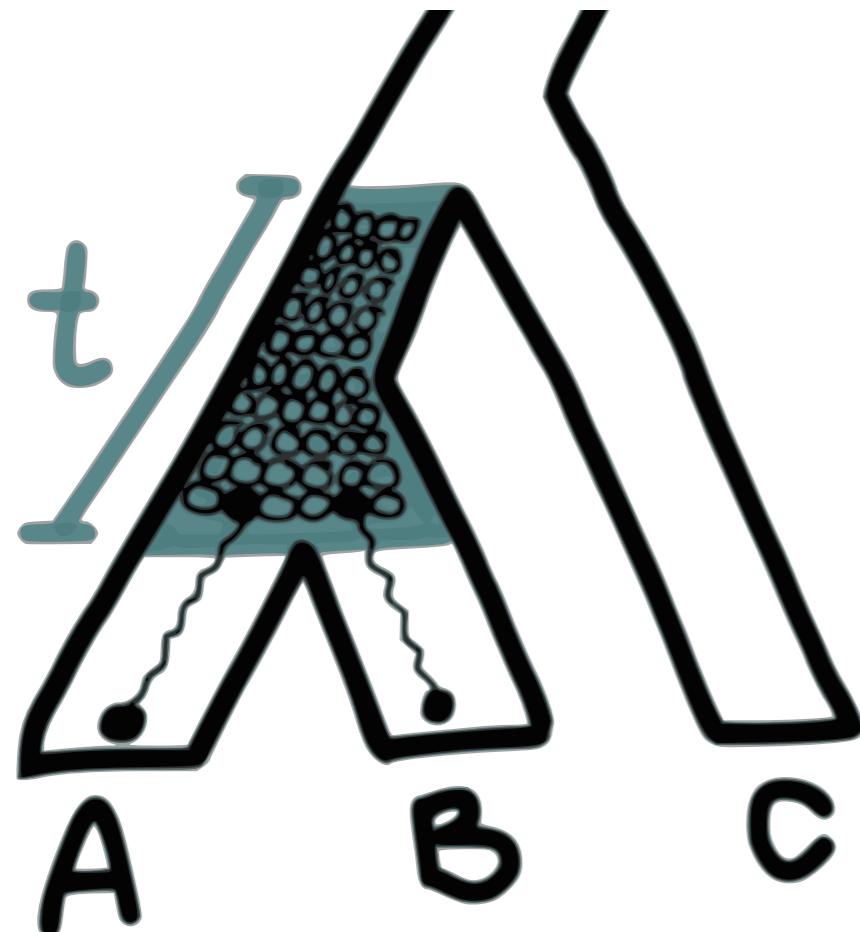
$$T = \frac{g}{N} \text{ coalescent units} \sim \text{Exp}(1)$$

Time to coalesce

$$P(T > t) = e^{-t}$$

Probability of no coalescence in time t

Multispecies coalescent on a tree



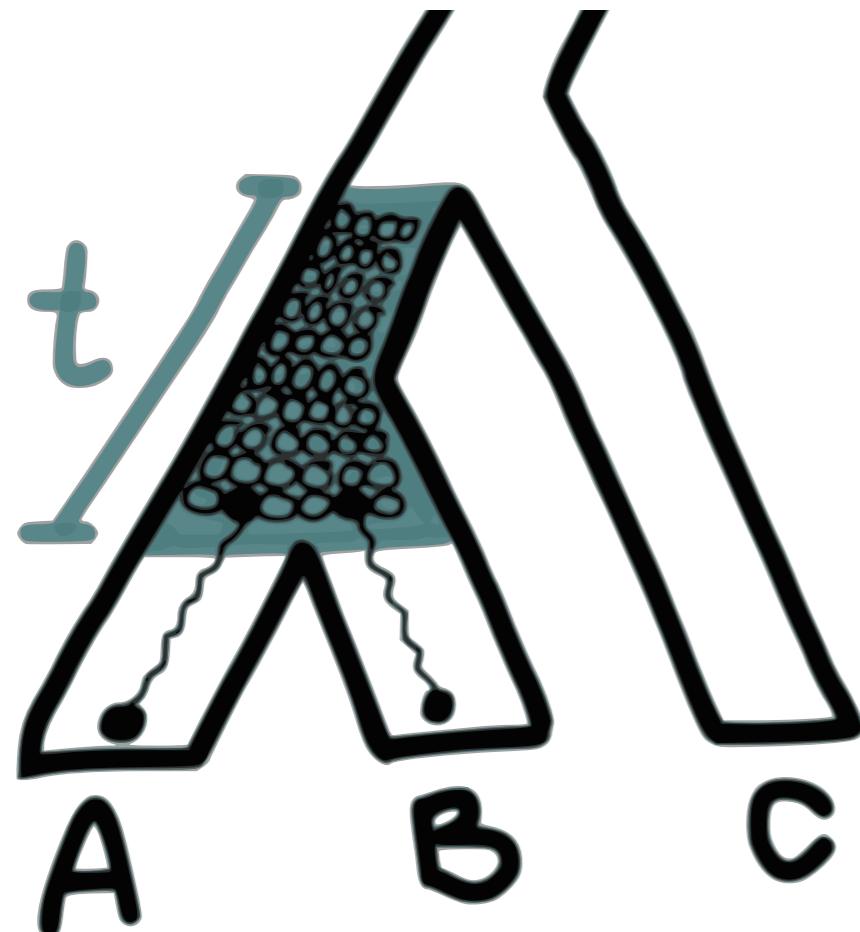
$$P(\text{ } \text{ } \text{ } \text{ } \text{ } \text{ }) =$$

A probability expression $P(\text{ } \text{ } \text{ } \text{ } \text{ } \text{ }) =$ followed by a phylogenetic tree diagram where the root node is labeled with a large Greek letter λ . Below the tree, the tips are labeled A, B, and C.

$$P(T > t) = e^{-t}$$

Probability of no
coalescence in time t

Multispecies coalescent on a tree

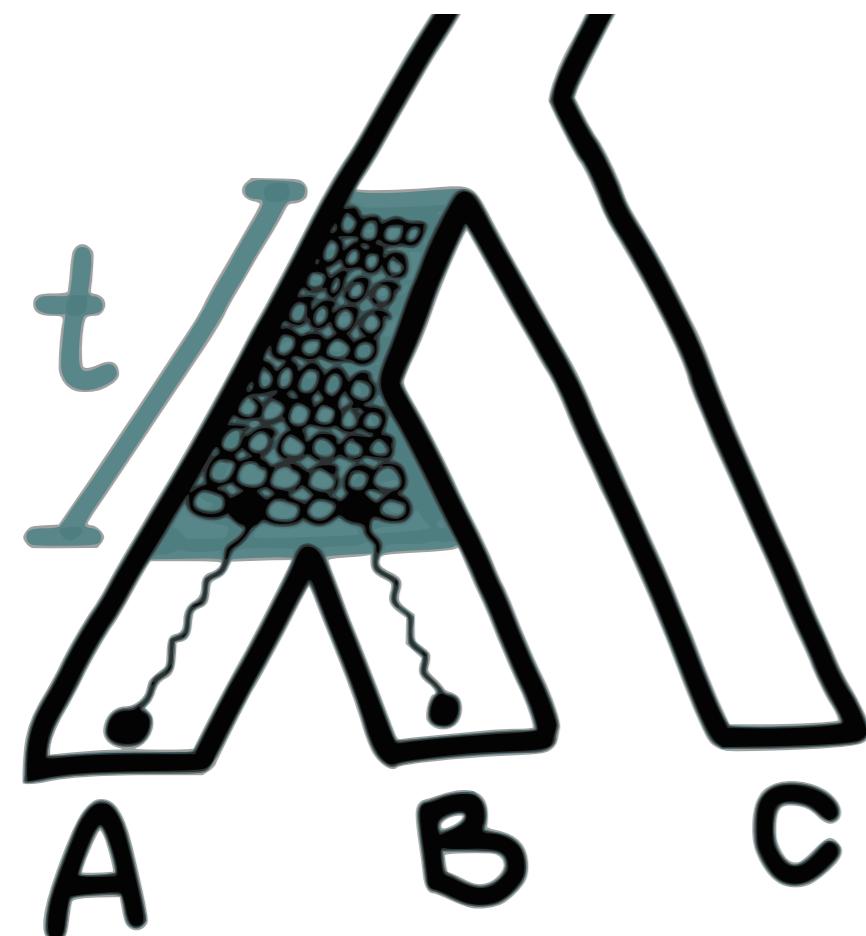


$$P(\wedge_{A B C}) = 1 - e^{-t}$$

$$P(T > t) = e^{-t}$$

Probability of no coalescence in time t

Multispecies coalescent on a tree

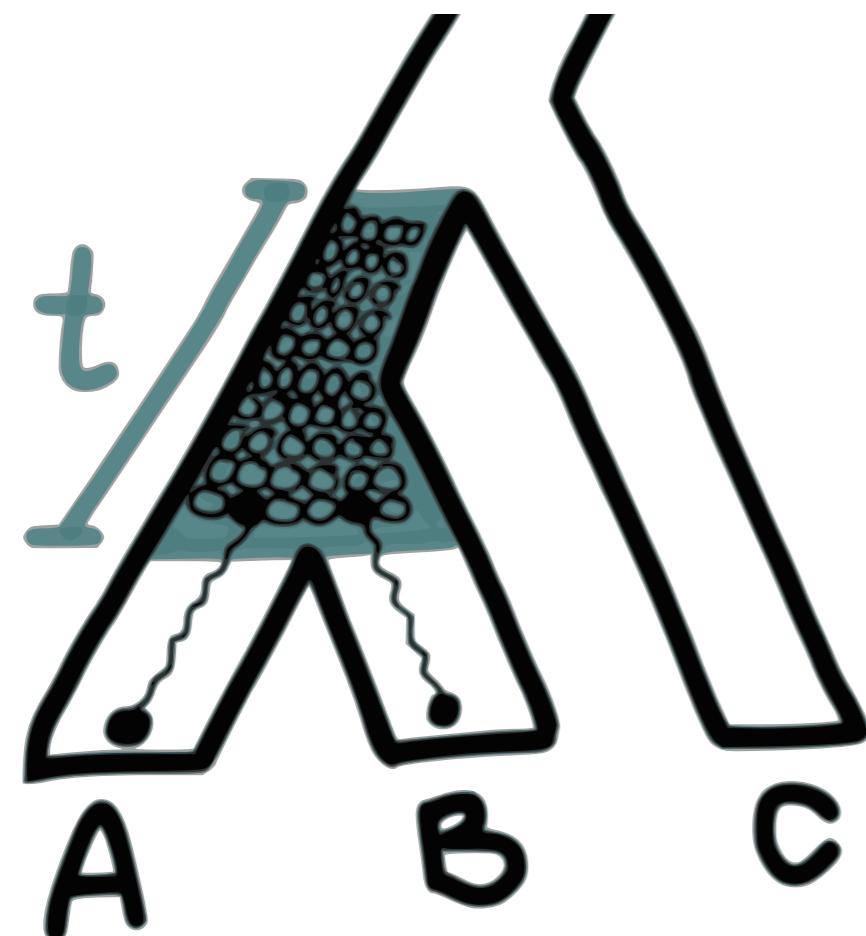


$$P(\wedge_{A B C}) =$$
$$1 - e^{-t}$$
$$+$$

$$P(T > t) = e^{-t}$$

Probability of no coalescence in time t

Multispecies coalescent on a tree

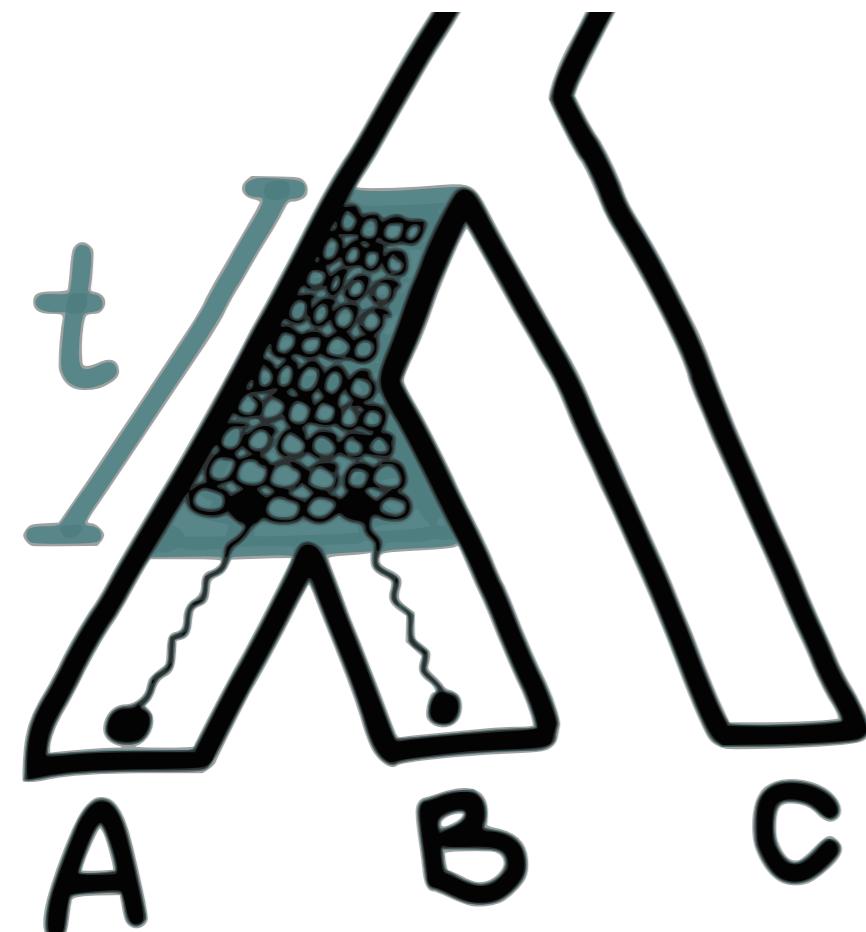


$$P(\text{ } \text{ } \text{ } \text{ } \text{ } \text{ }) = \\ 1 - e^{-t} \\ + \\ e^{-t} \times 1/3$$

$$P(T > t) = e^{-t}$$

Probability of no
coalescence in time t

Multispecies coalescent on a tree

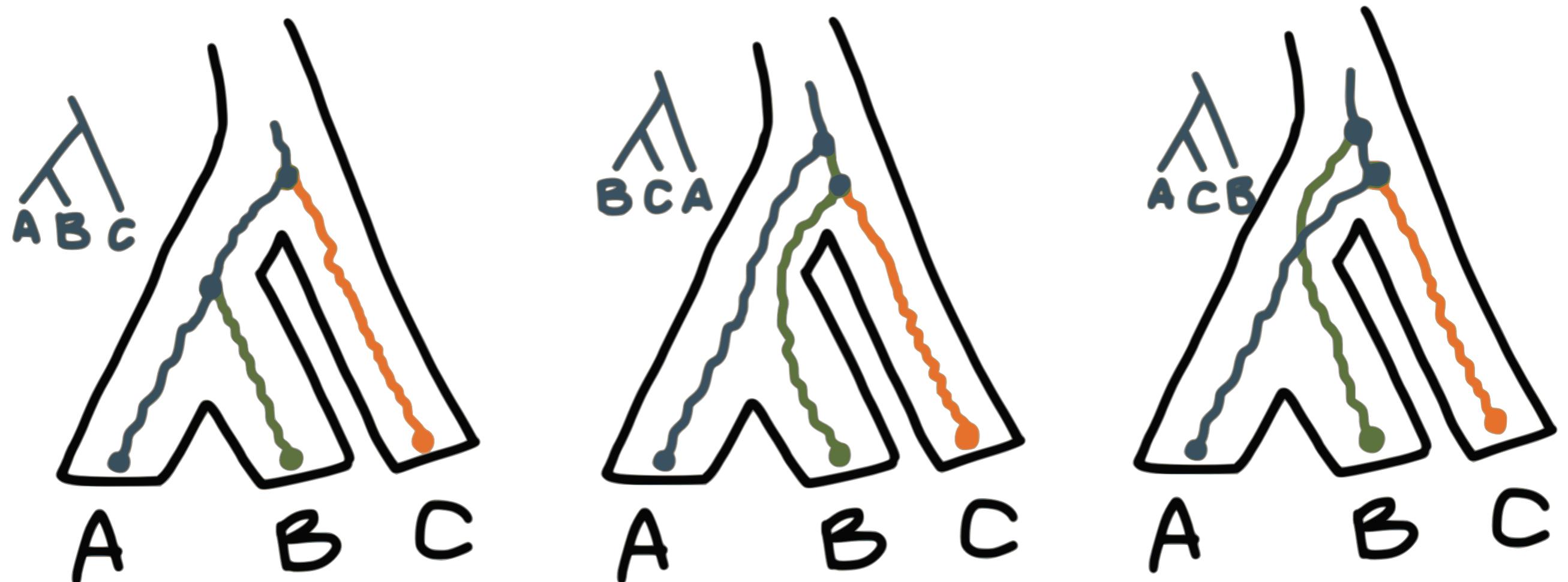


$$P(T > t) = e^{-t}$$

Probability of no coalescence in time t

$$\begin{aligned}
 P(\bigwedge_{A B C}) &= \\
 1 - e^{-t} + e^{-t} \times 1/3 &= \\
 = 1 - \frac{2}{3}e^{-t}
 \end{aligned}$$

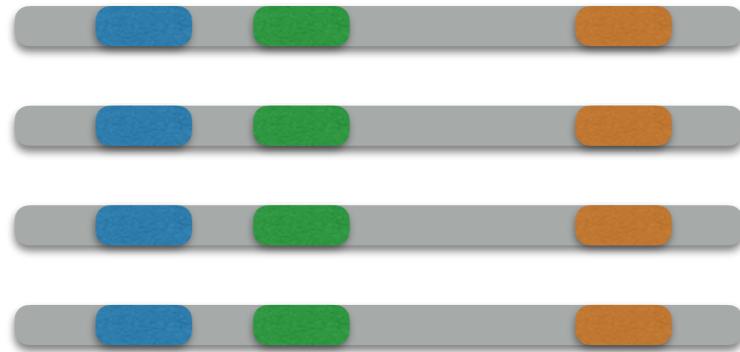
Multispecies coalescent on a tree



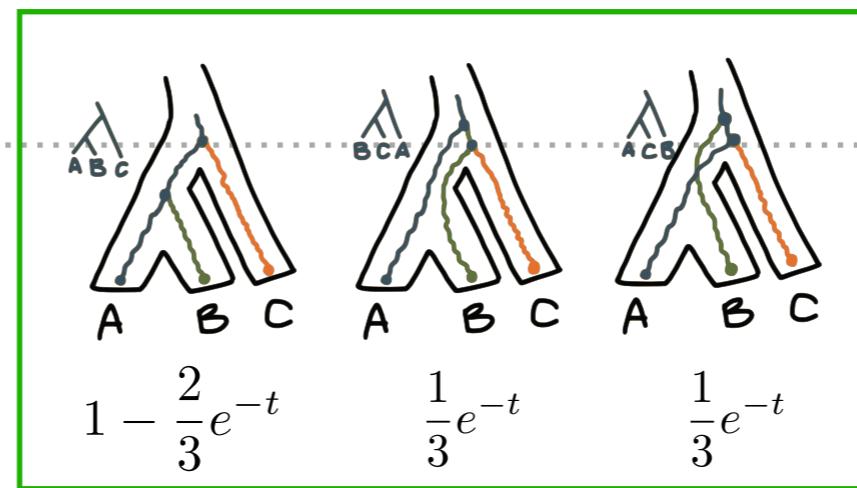
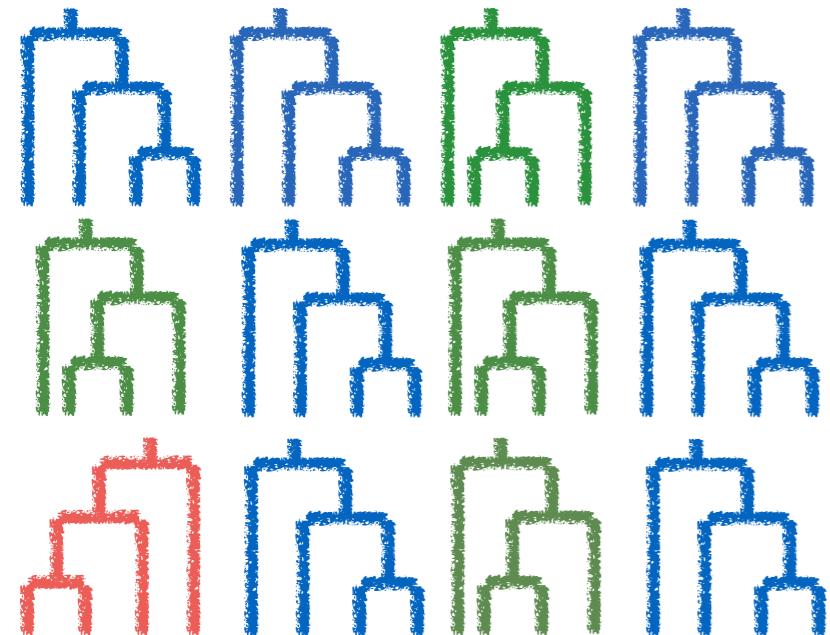
$$1 - \frac{2}{3}e^{-t}$$

$$\frac{1}{3}e^{-t}$$

$$\frac{1}{3}e^{-t}$$

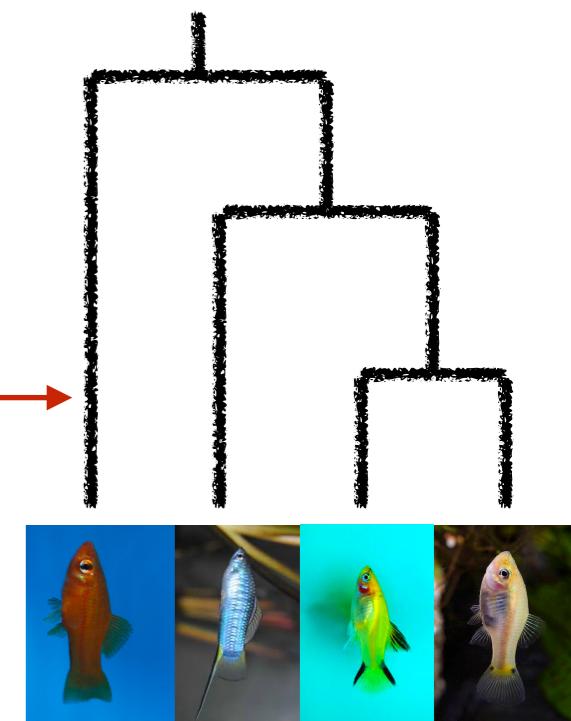


Distances
Parsimony
Likelihood
(Bayesian)

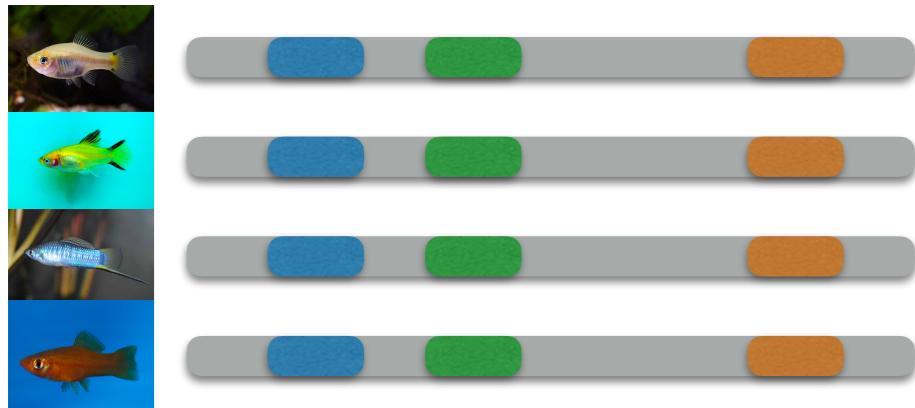


$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

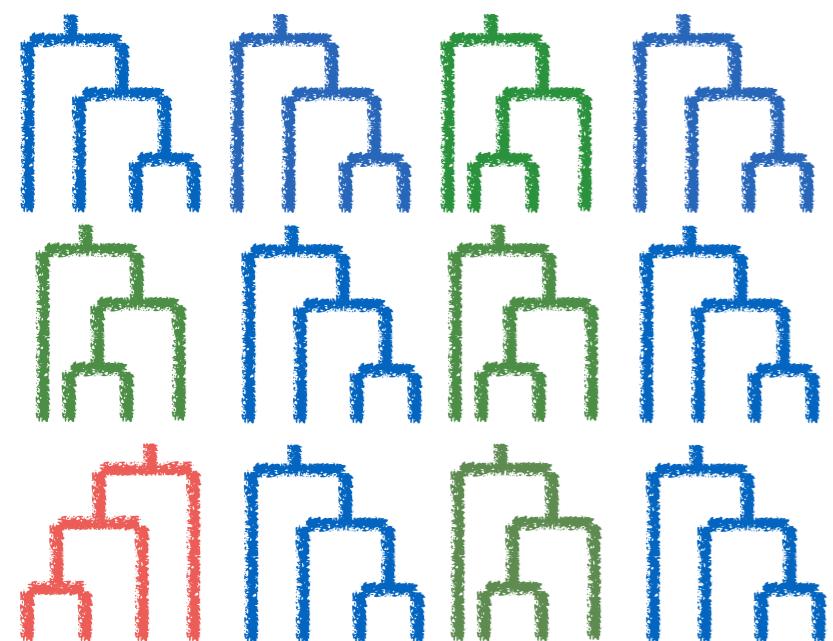
Max. Lik.



Data



Distances
Parsimony
Likelihood
(Bayesian)

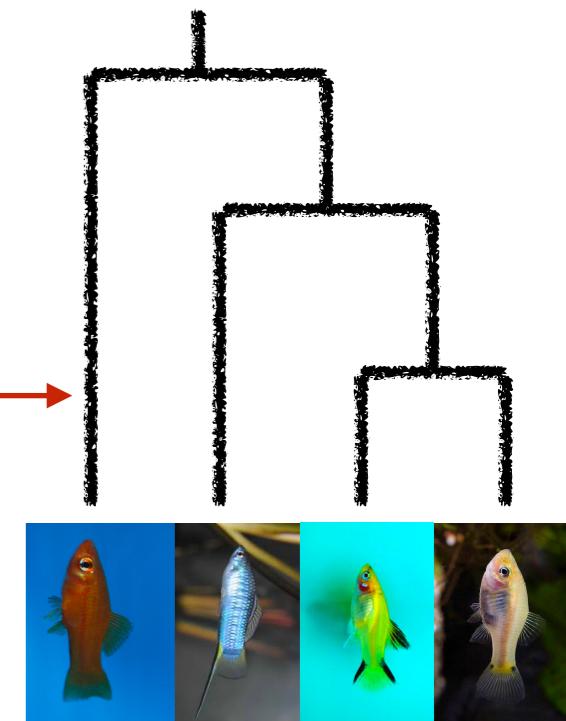


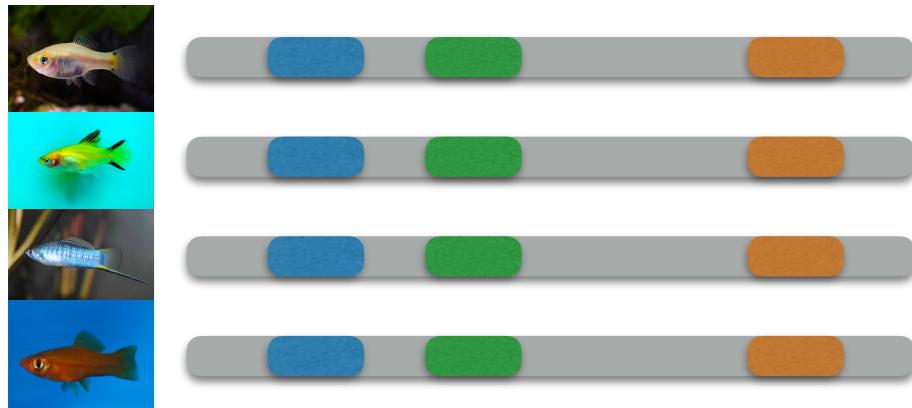
Data

$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

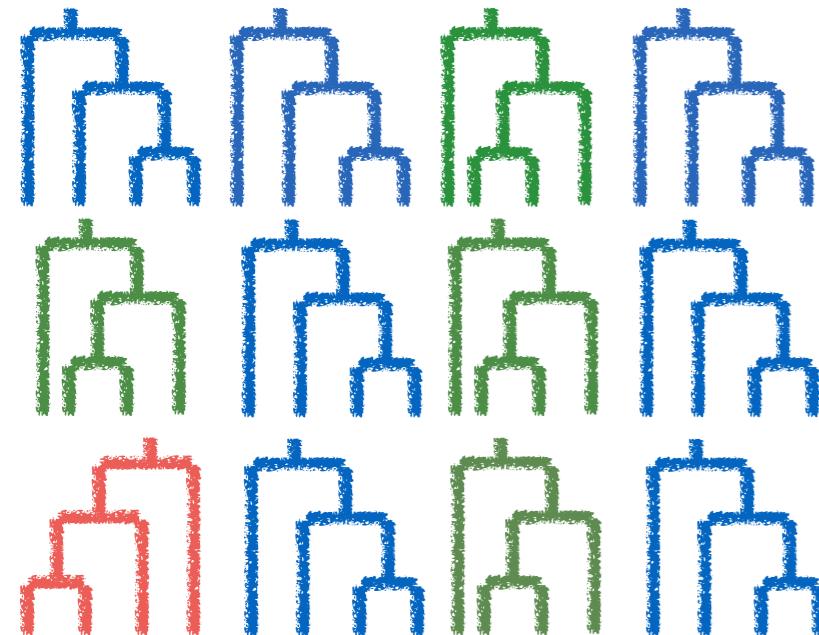
Max. Lik.

1. Guess a species tree
2. Evaluate likelihood of data (gene trees) given species tree
3. Search space of trees for species tree that maximizes likelihood





Distances
Parsimony
Likelihood
(Bayesian)



$$P(T, \theta | G) \propto \pi(T) \pi(\theta) \prod_{i=1}^L P(G_i | T, \theta)$$

Prior Tree Multispecies Coalescent

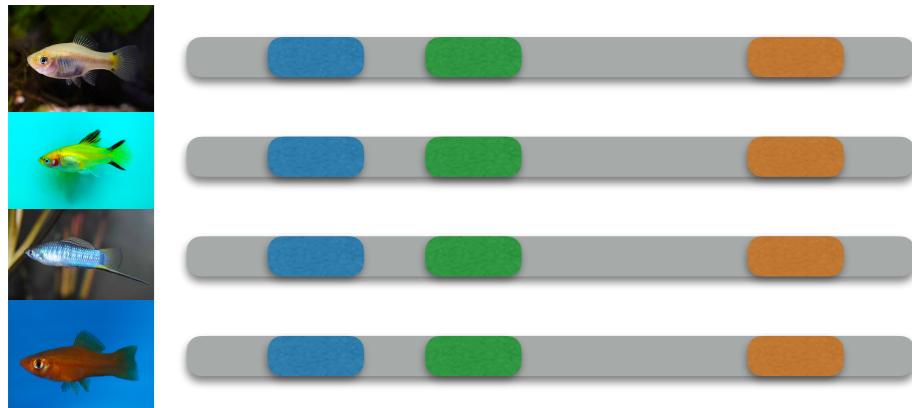
Bayesian



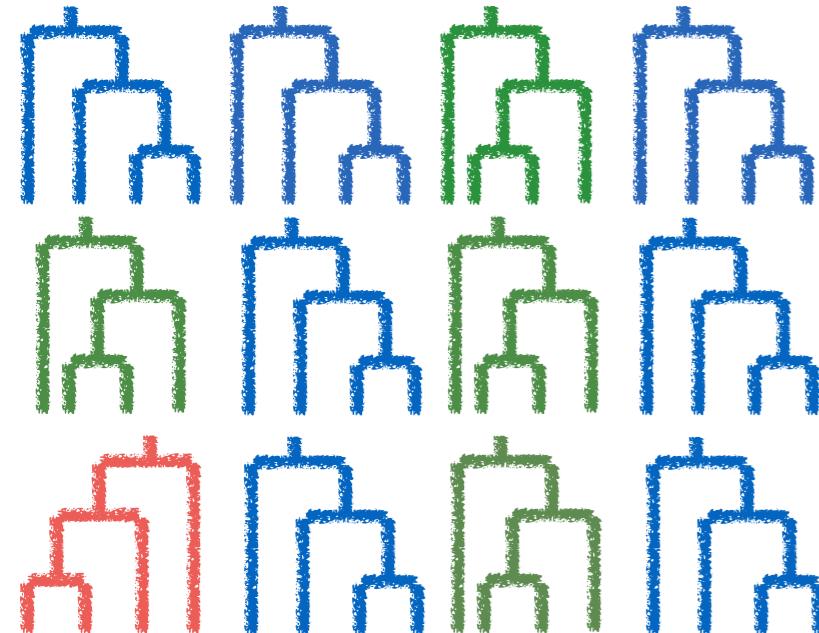
$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

Max. Lik.

Summary methods: ASTRAL, BUCKy, MP-EST
 (Zhang et al, 2018) (Larget et al, 2010) (Liu et al, 2010)



Distances
Parsimony
Likelihood
(Bayesian)



$$P(T, \theta | G) \propto \pi(T) \pi(\theta) \prod_{i=1}^L P(G_i | T, \theta)$$

Prior Tree Multispecies Coalescent



$$L(T, \theta) = \prod_{i=1}^L P(G_i | T, \theta)$$

Bayesian

Max. Lik.

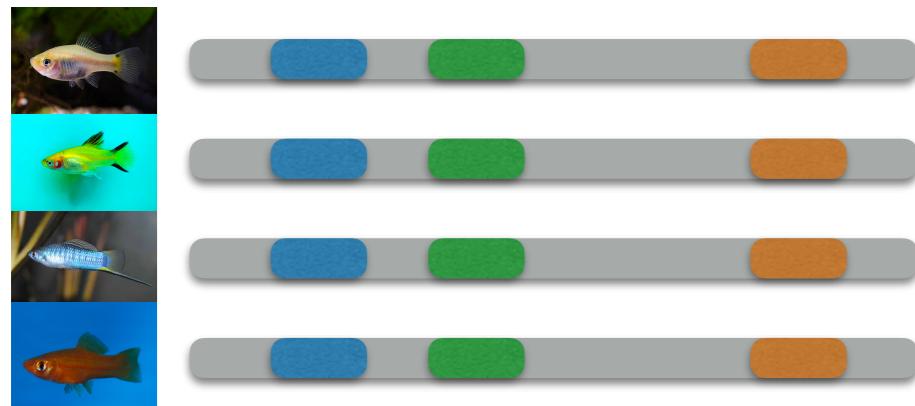
Summary methods: ASTRAL, BUCKy,
(Zhang et al, 2018) (Larget et al, 2010)

Do not search tree space

Approx lik

MP-EST
(Liu et al, 2010)

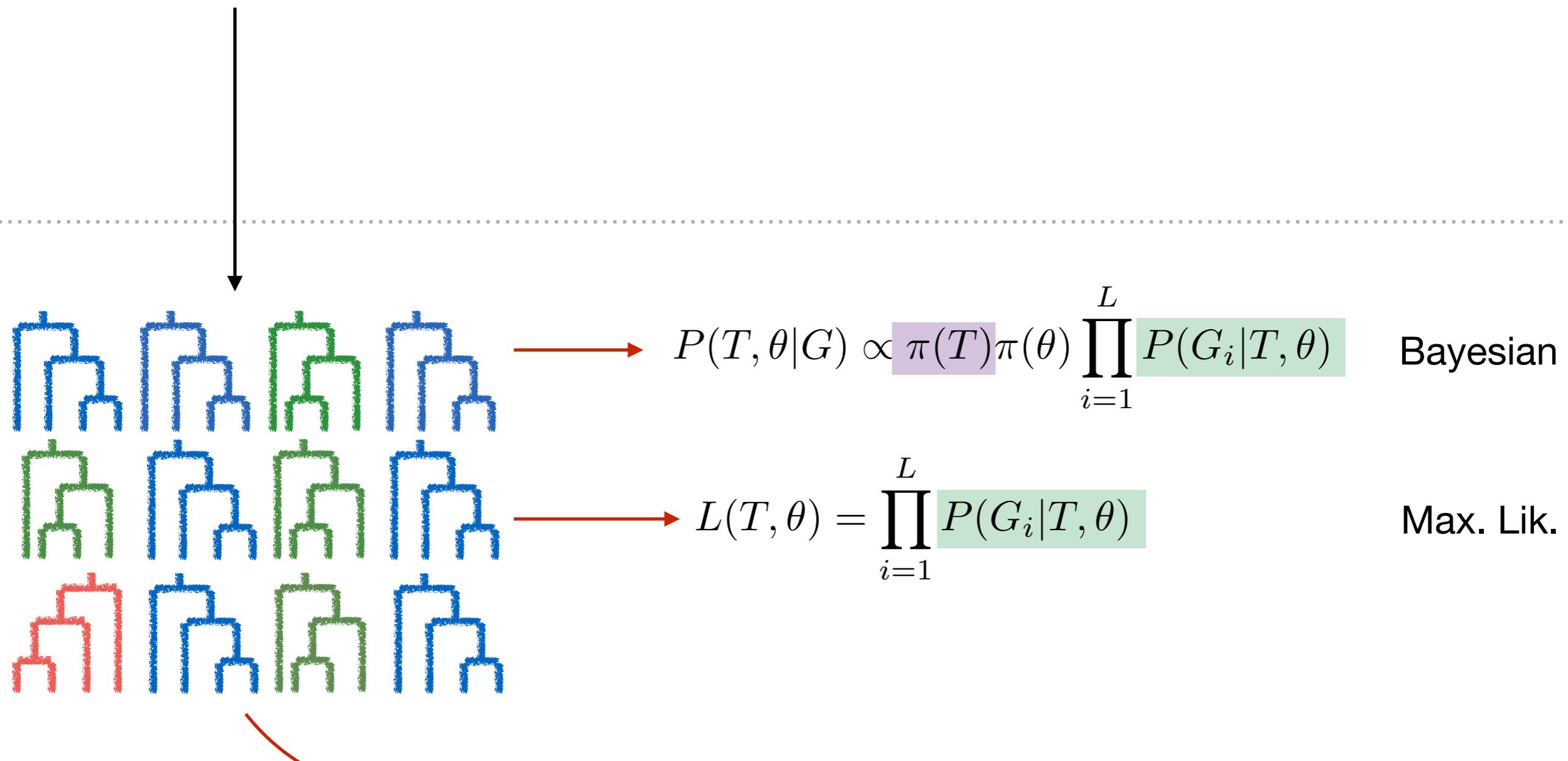
Co-estimation (lecture 15)



$$P(T, G, \theta | D) \propto \pi(T)\pi(\theta) \prod_{i=1}^L P(D_i | G_i)P(G_i | T)$$

Tree
gene trees L loci
↑ ↑
Prior Tree

Substitution Model **Multispecies Coalescent**



Summary methods: ASTRAL, BUCKy, MP-EST
 (Larget et al, 2010) (Liu et al, 2010)

Anomaly zone

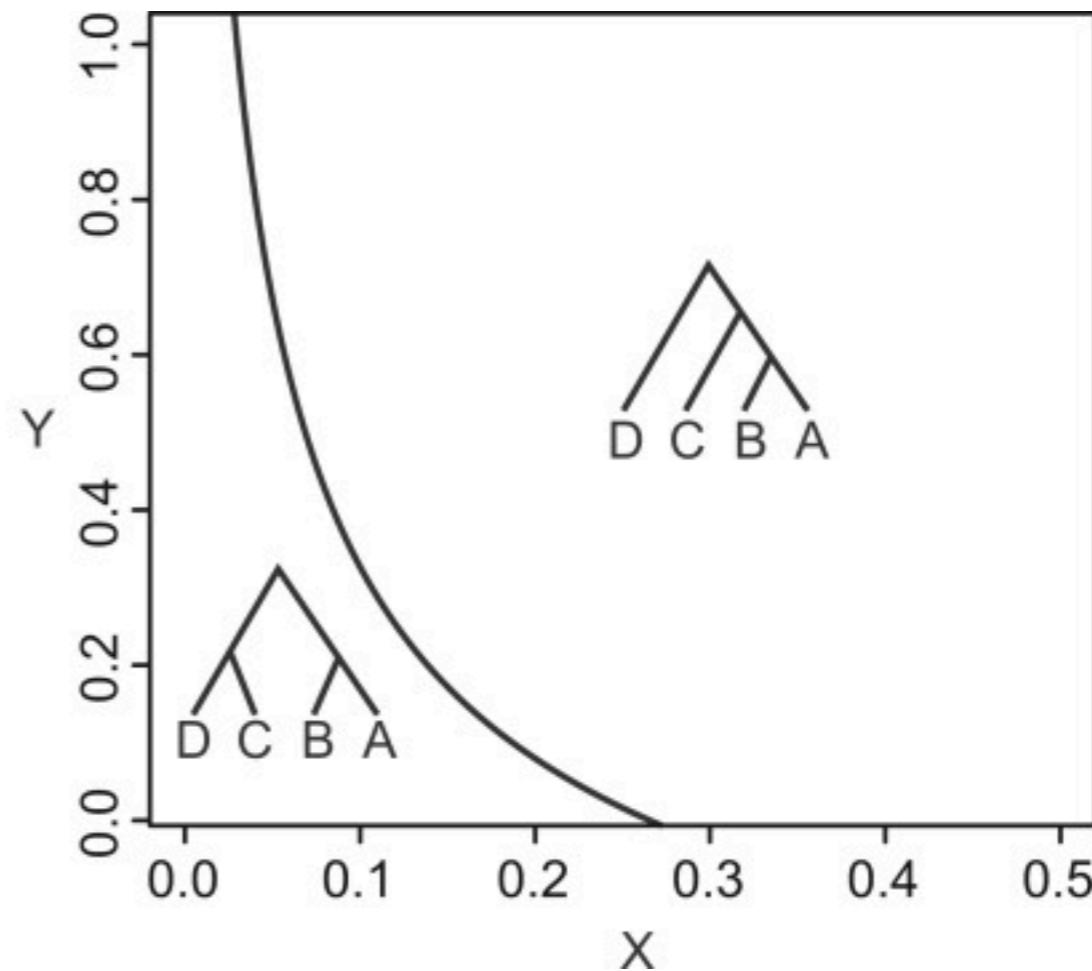
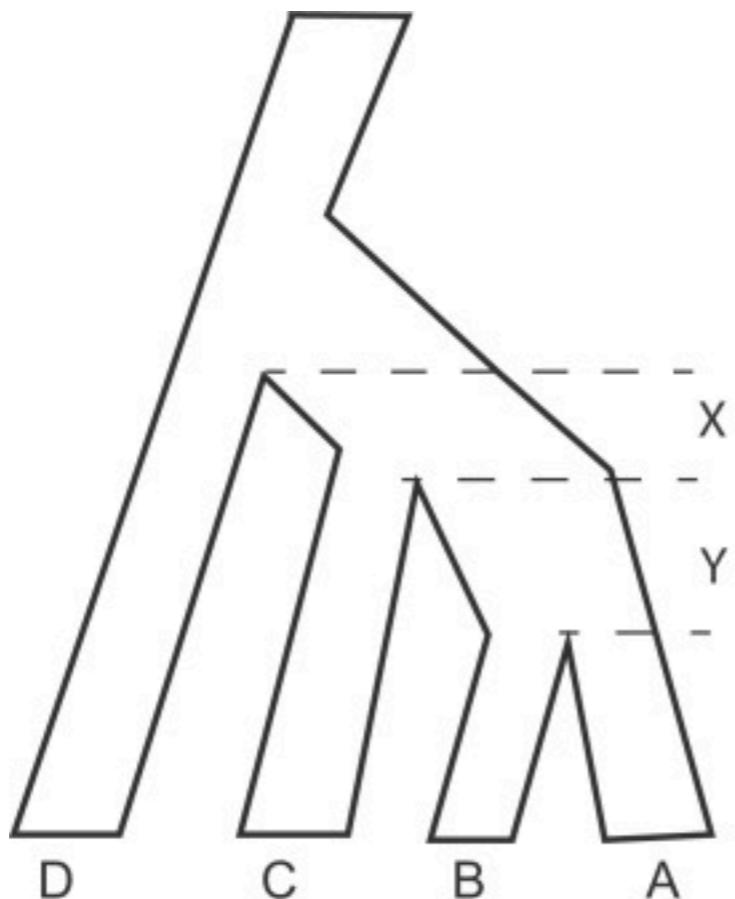
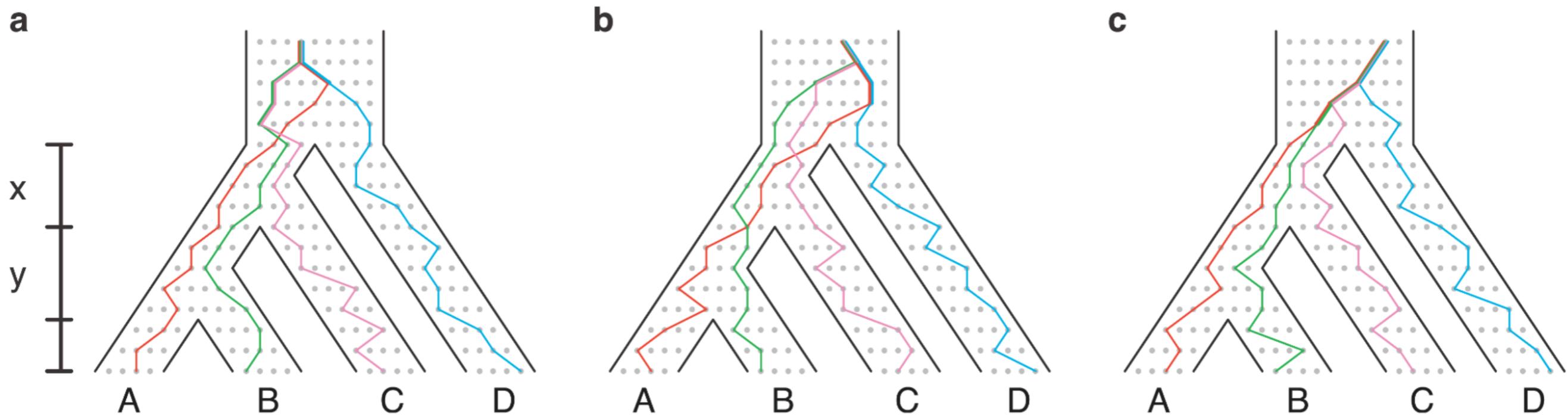
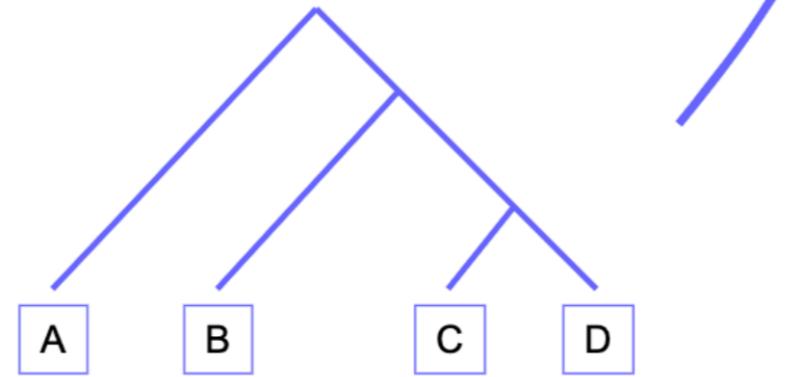
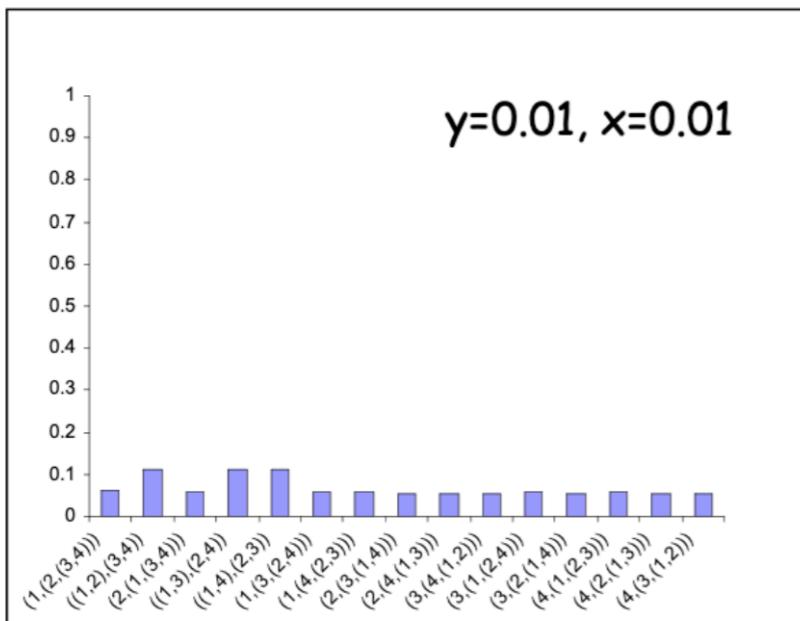
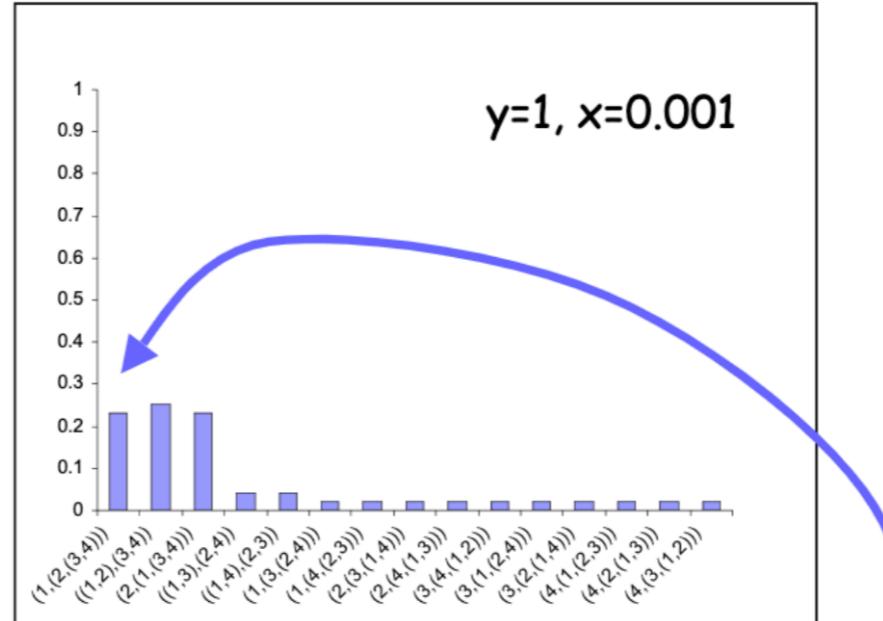
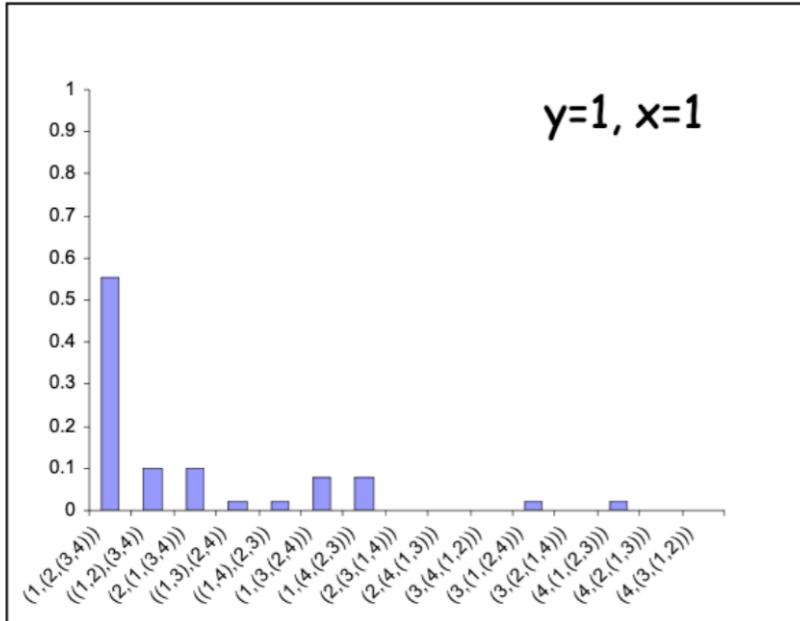
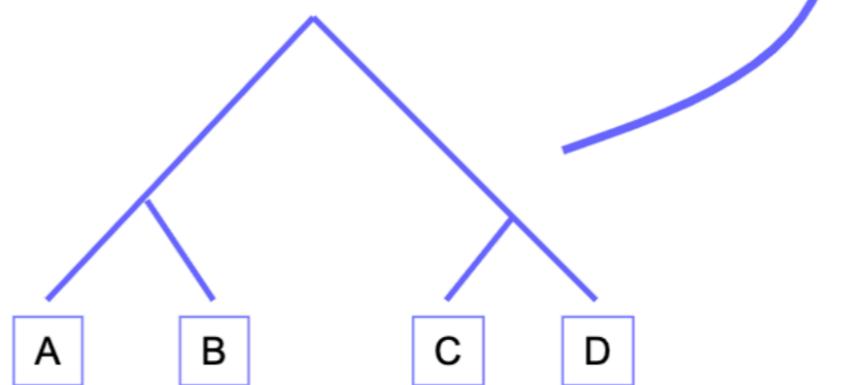
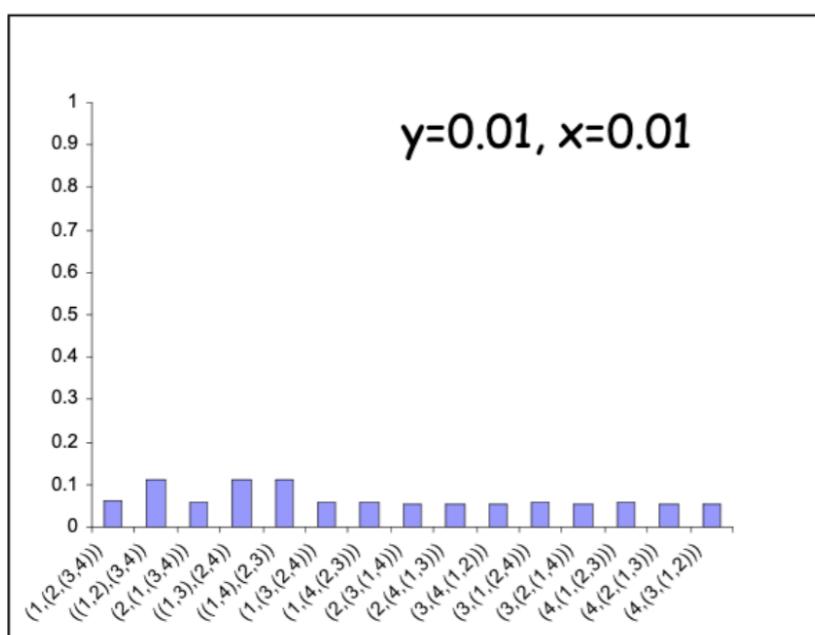
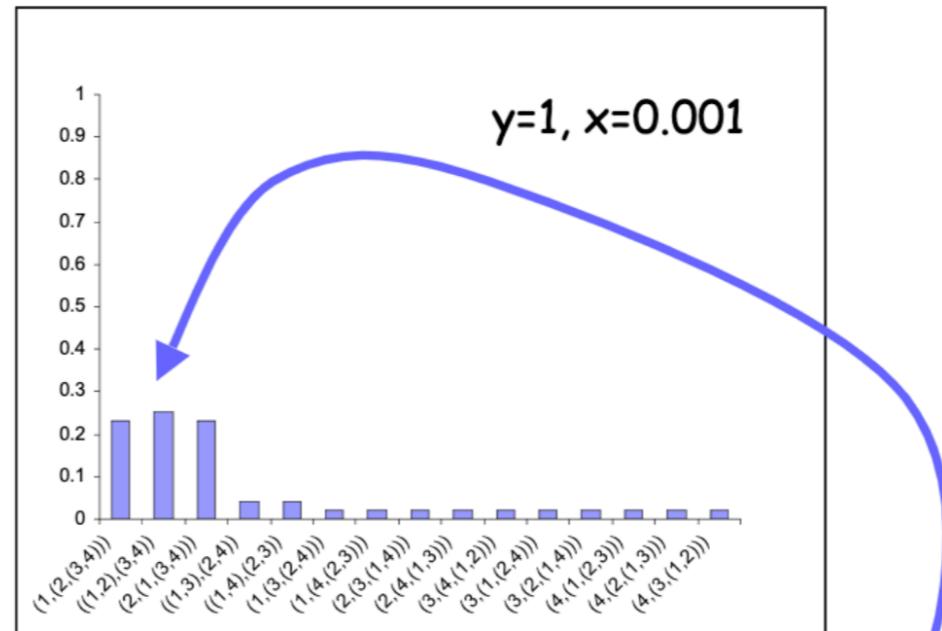
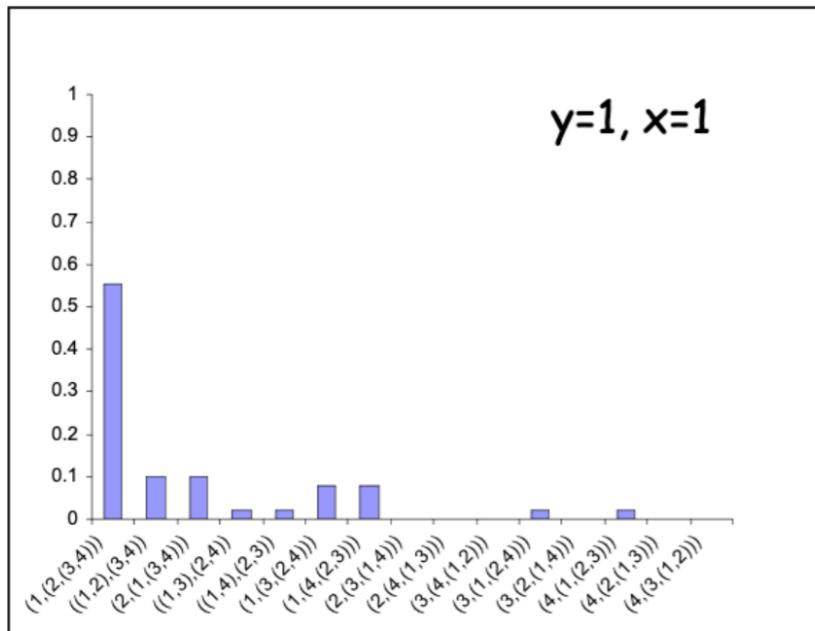


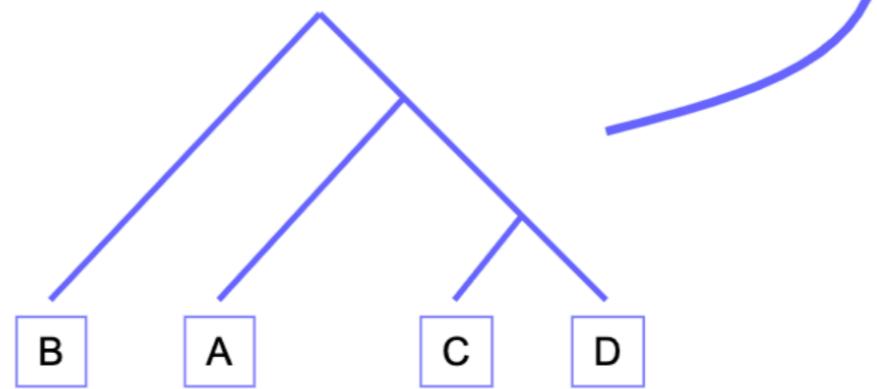
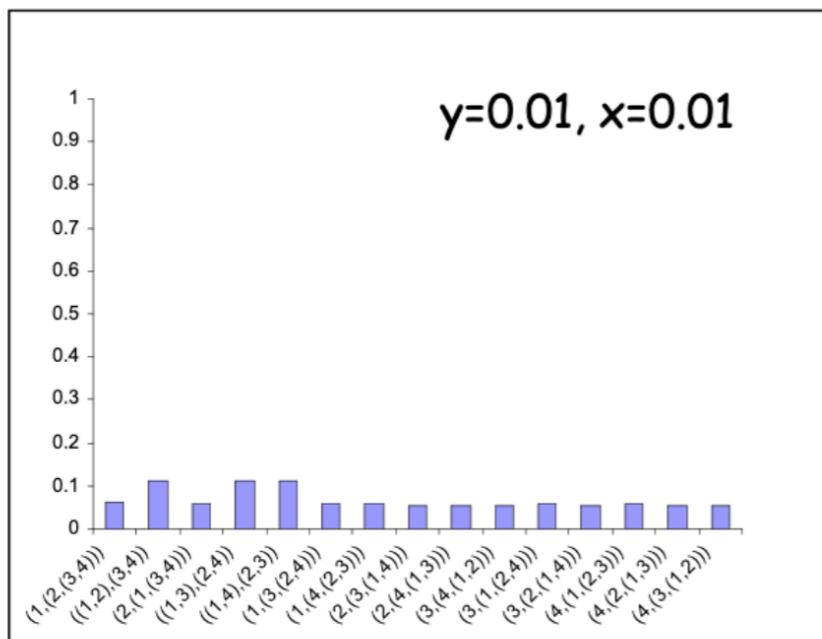
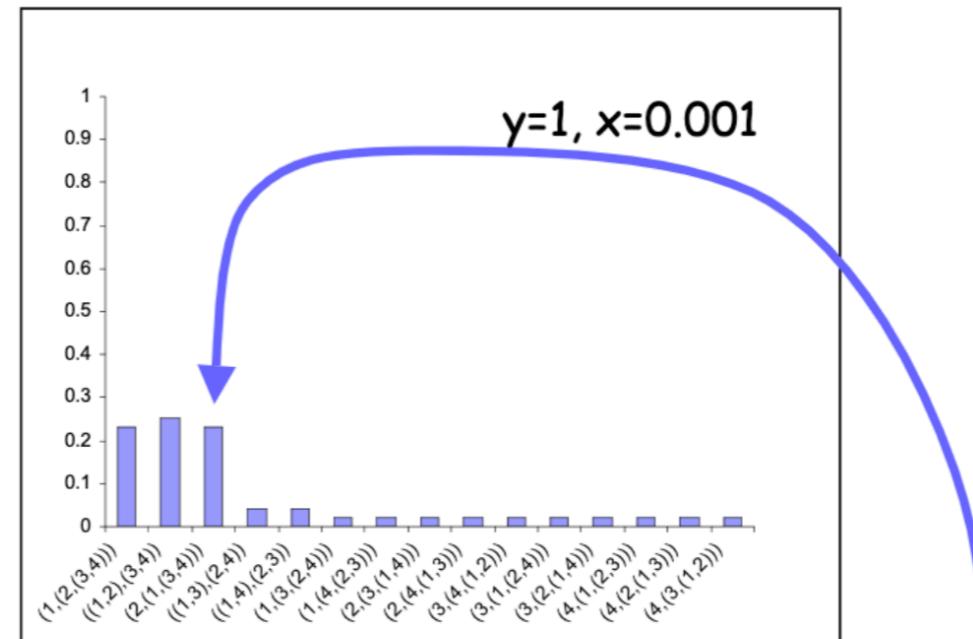
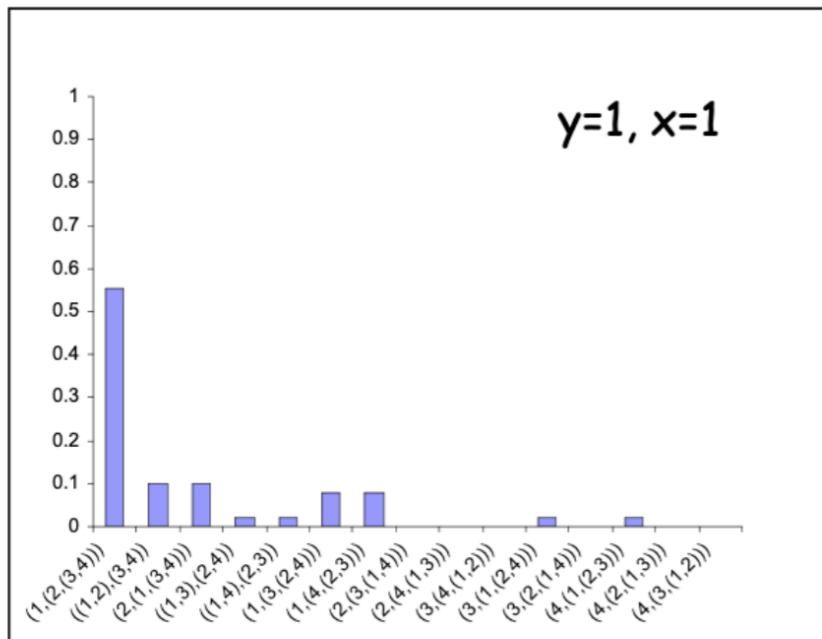
Figure 1 in [Linkem et al \(2016\)](#)



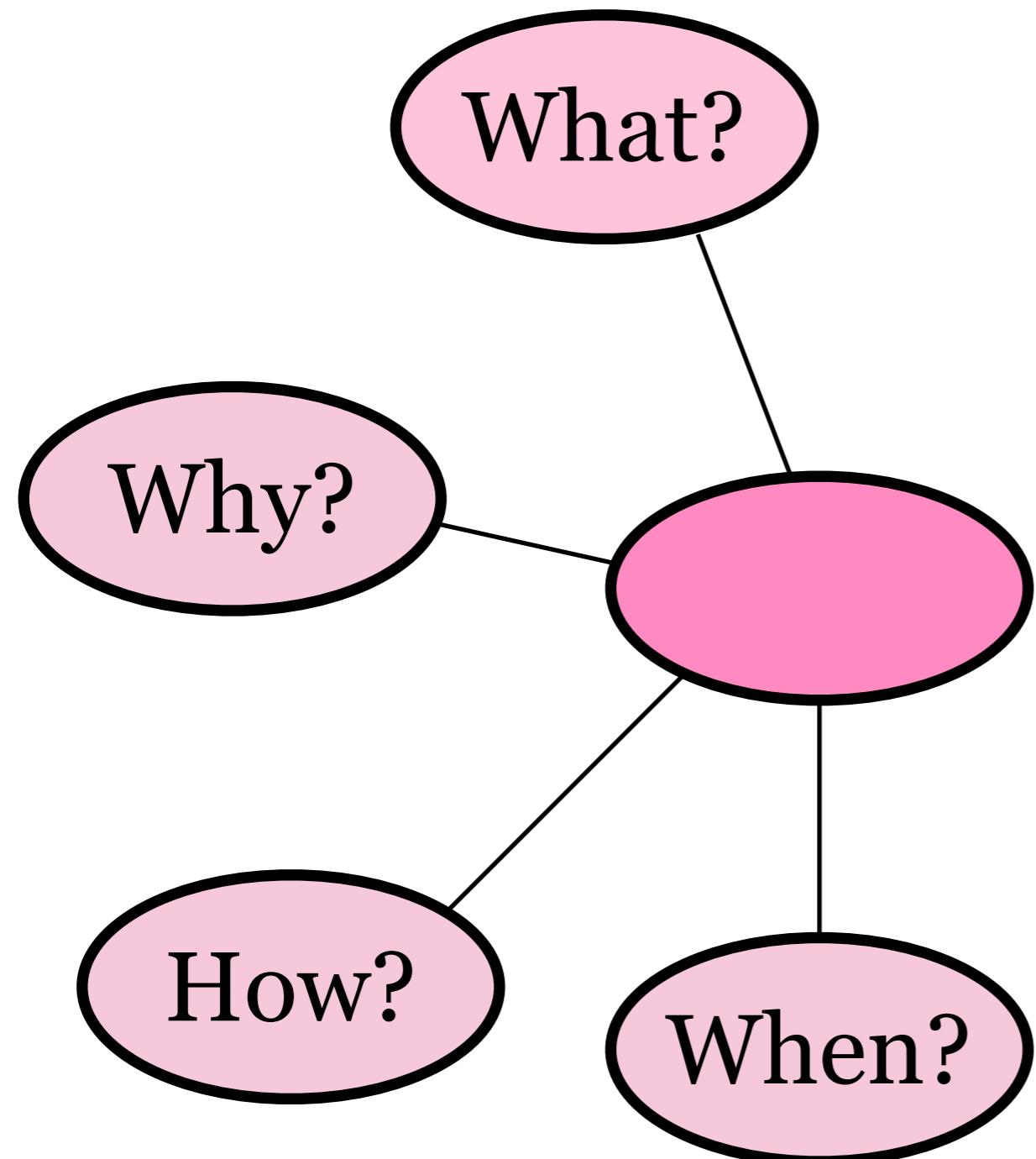
If the internal branches of the species tree— x and y —are short so that coalescences occur deep in the tree, the two sequences of coalescences that produce a given symmetric gene tree topology together have higher probability than the single sequence that produces the topology that matches the species tree. (a) and (b) Two coalescence sequences leading to gene tree topology $((AD)(BC))$. In (a), the lineages from B and C coalesce more recently than those from A and D, and in (b), the reverse is true. (c) The single sequence of coalescences leading to gene tree topology $((AB)C)D$. (Degnan and Rosenberg, 2006)







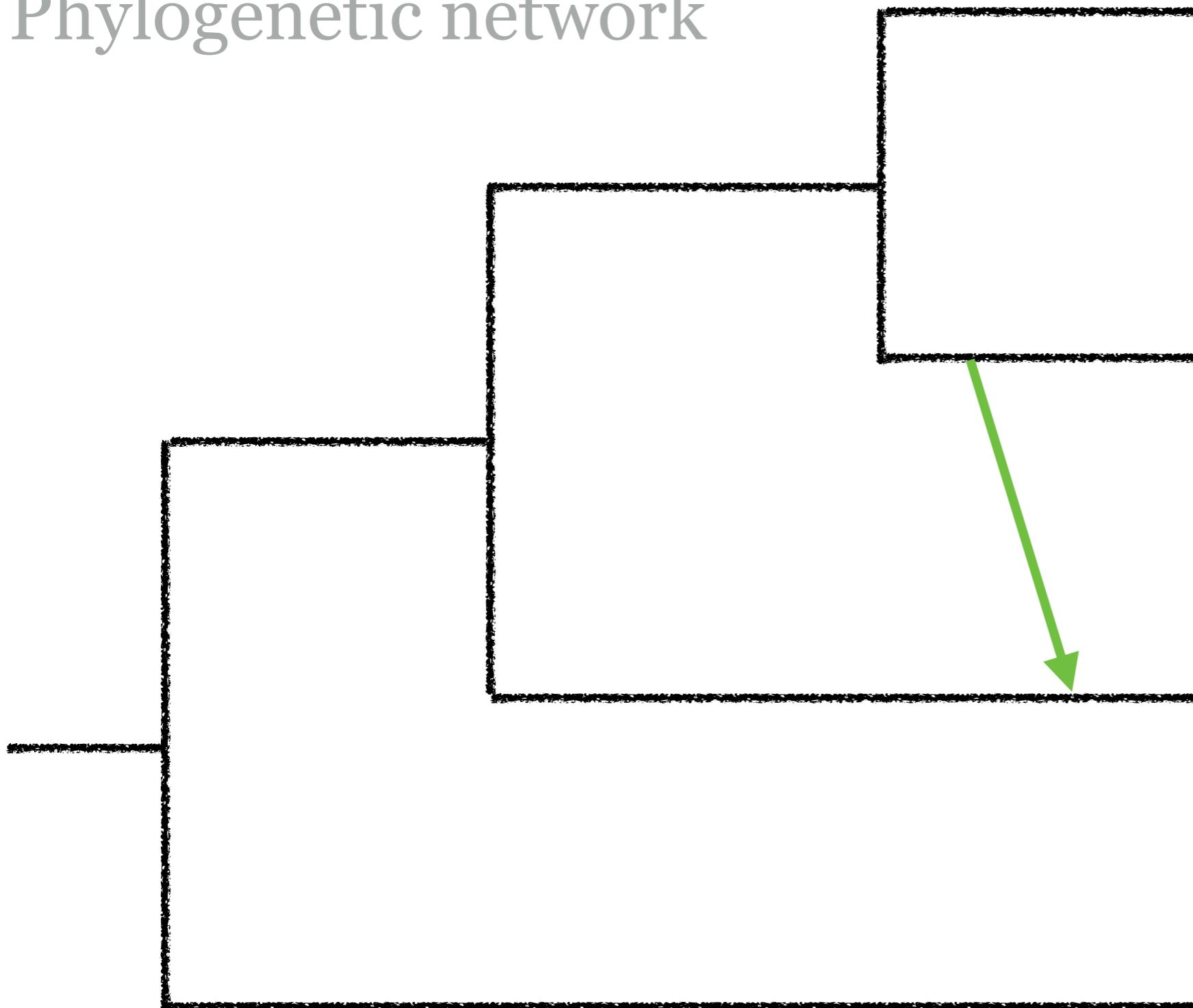
- Concatenation: assumes all genes follow the same tree-like history
- Coalescent-based tree methods: accounts for ILS (and sometimes gene tree estimation error), but does not allow for other sources of gene tree discordance (like GDL or gene flow)
- Extensions to coalescent-based tree methods:
 - Coalescent-based network methods: accounts for ILS, gene tree estimation error and gene flow
 - Coalescent+GDL methods (Li et al, 2020)



Phylogenetic Networks

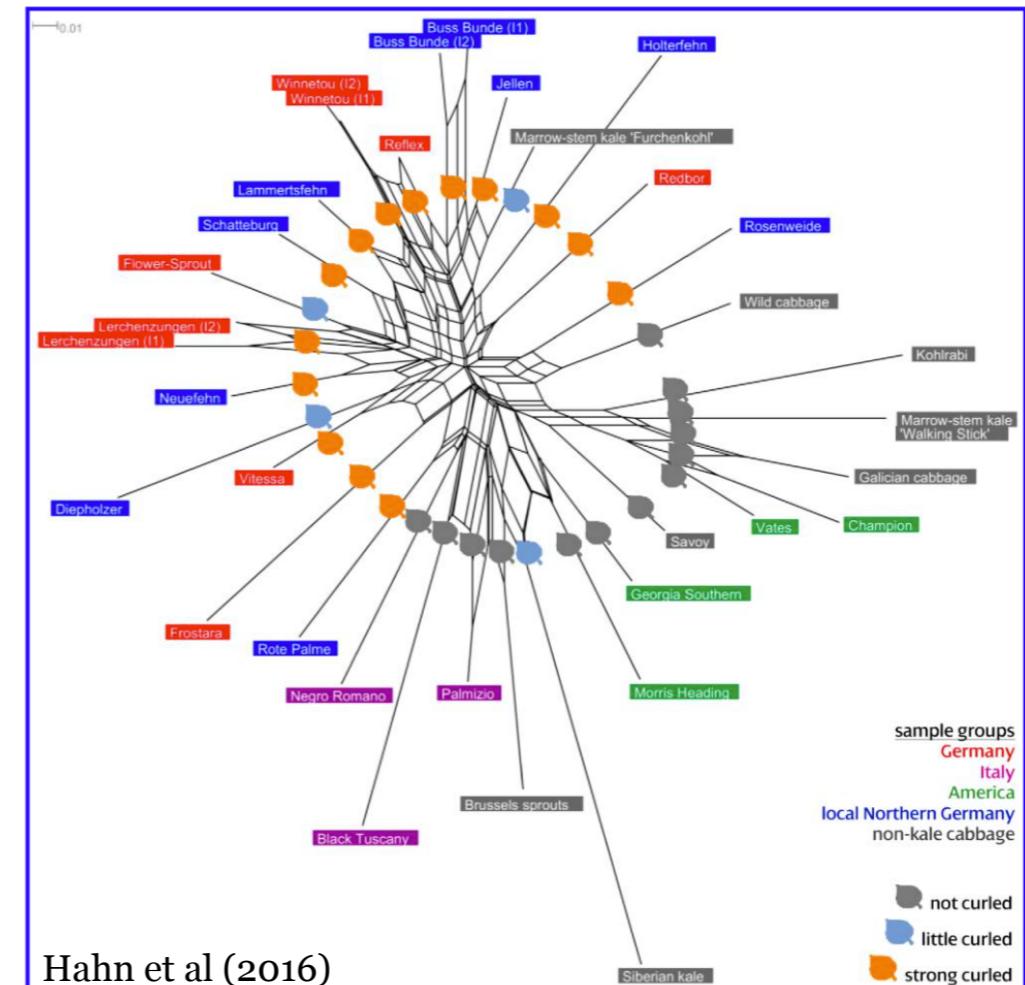
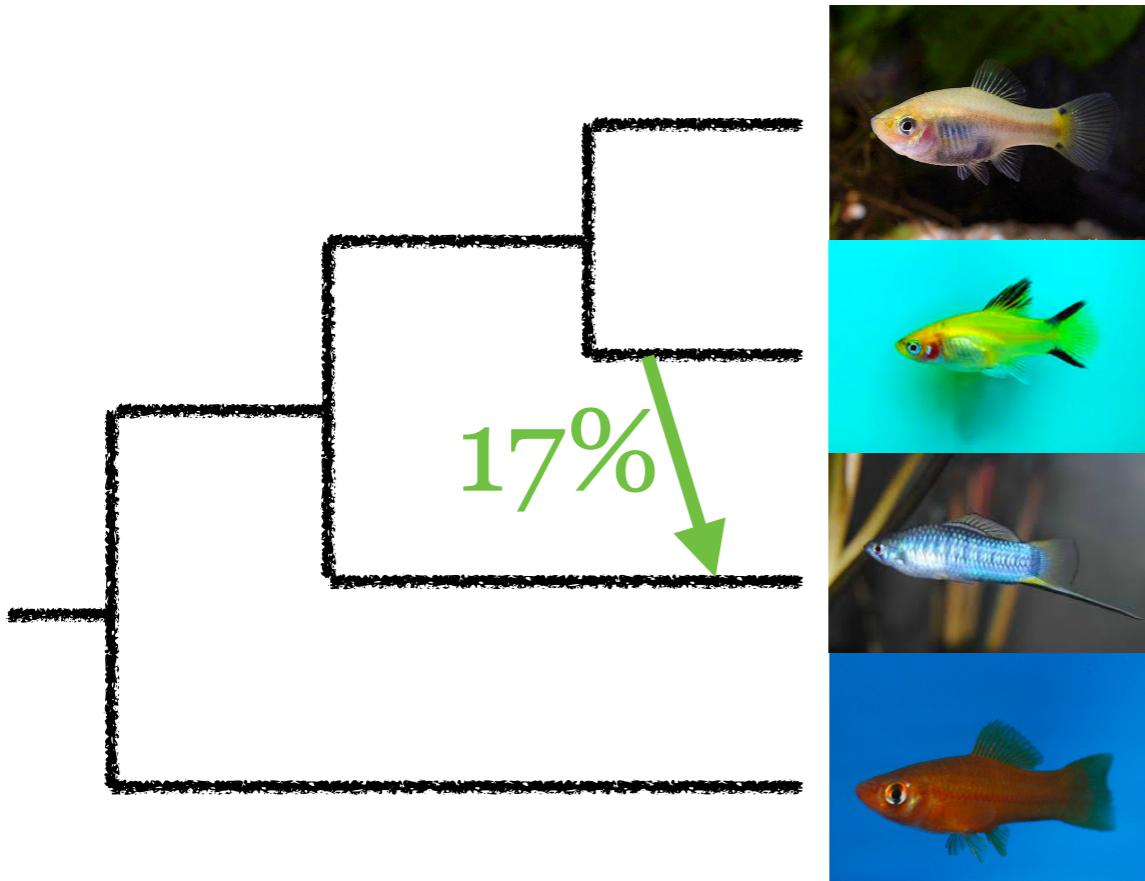
What?

Phylogenetic network



What?

Phylogenetic network

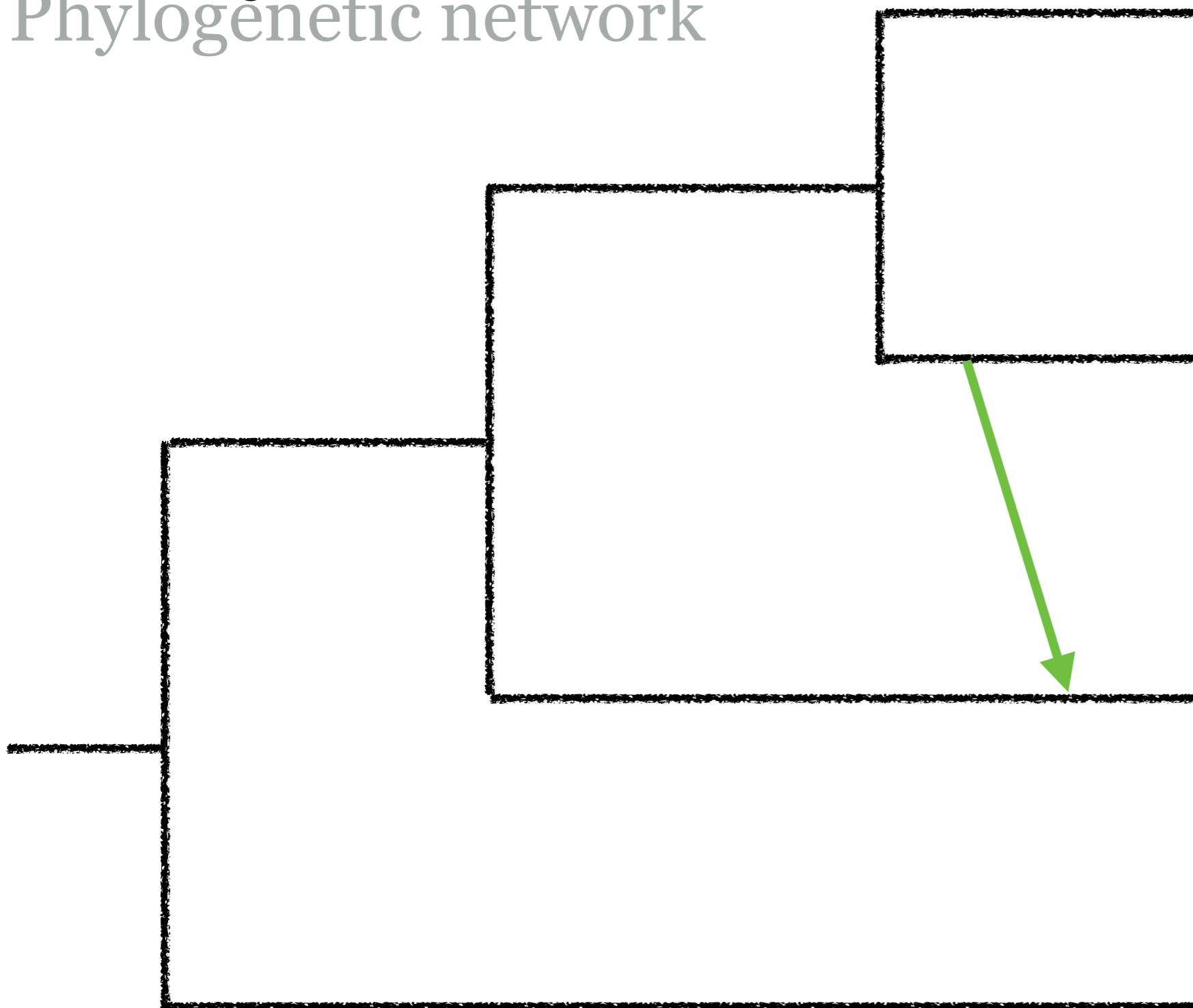


Explicit

Implicit

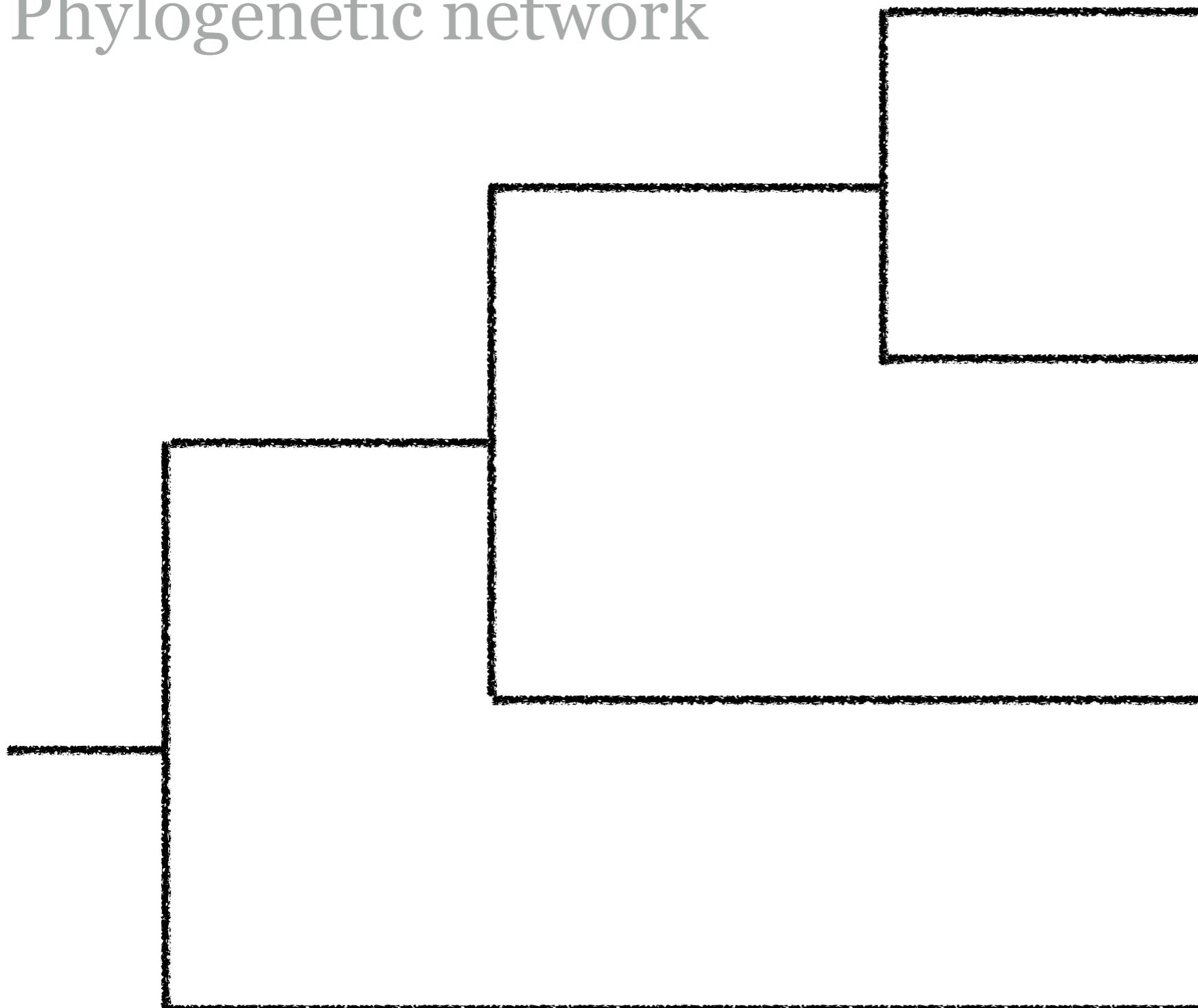
Why?

Phylogenetic network



Why?

Phylogenetic network



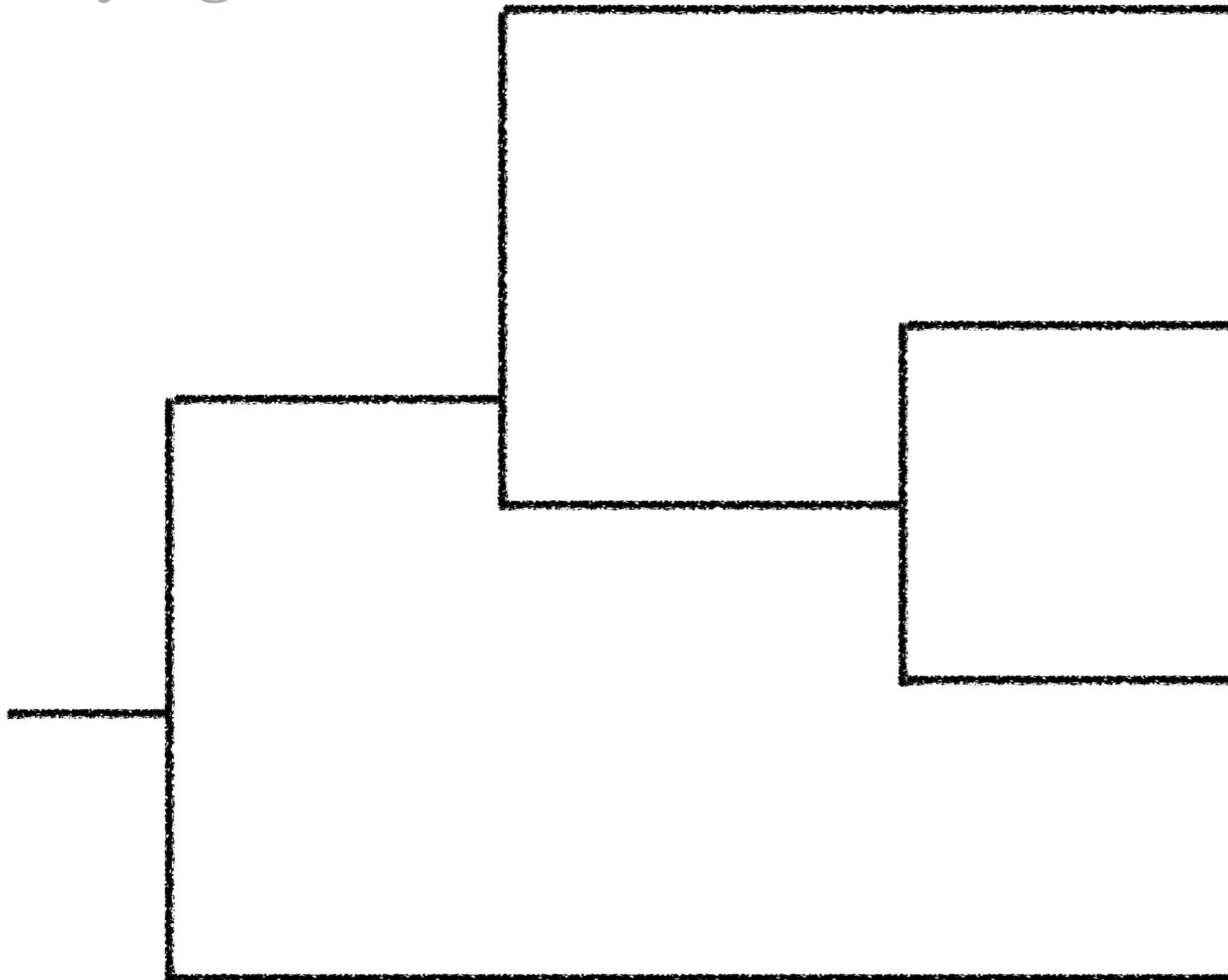
Main tree



Why?

Phylogenetic network

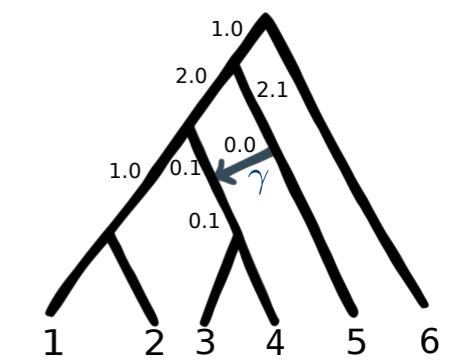
Ignore gene flow
=>Wrong tree!



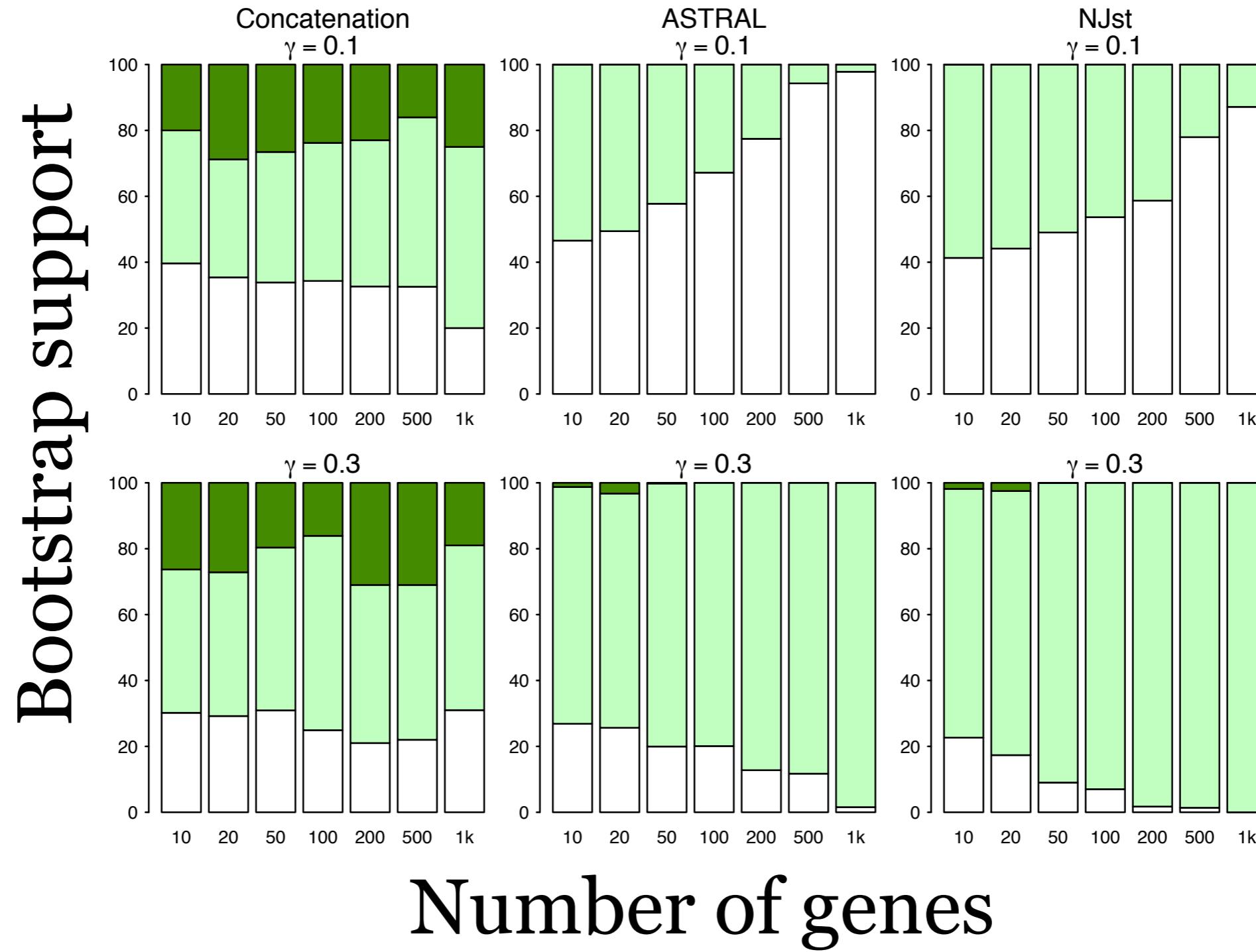
Why?

Phylogenetic network

Coalescent tree methods
not robust to gene flow



White:
true tree

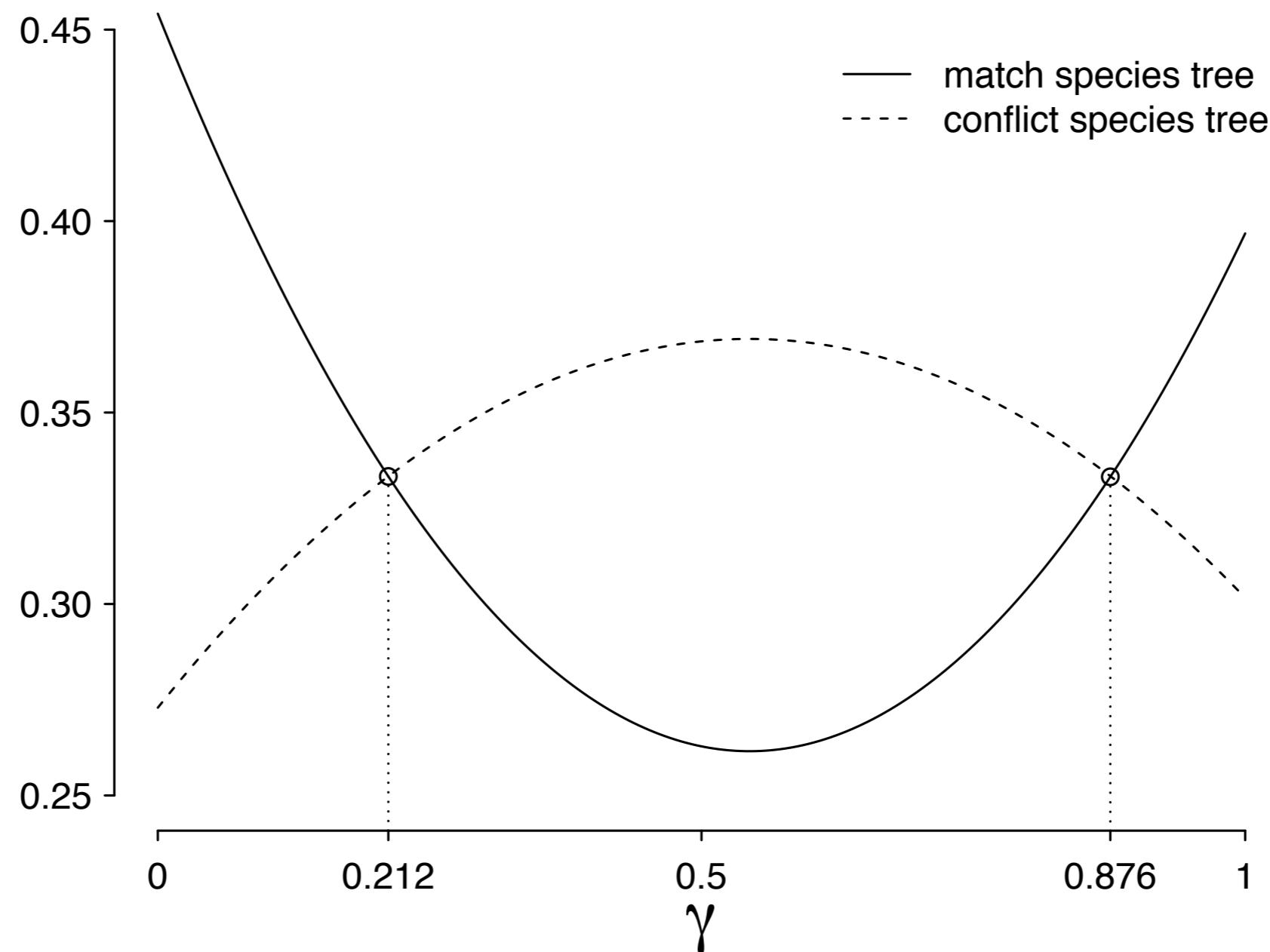


(S.-L., Yang, Ané, 2016, Syst Bio)

ASTRAL (Mirarab et al, 2014)
NJst (Liu&Yu, 2011)

Why? Phylogenetic network

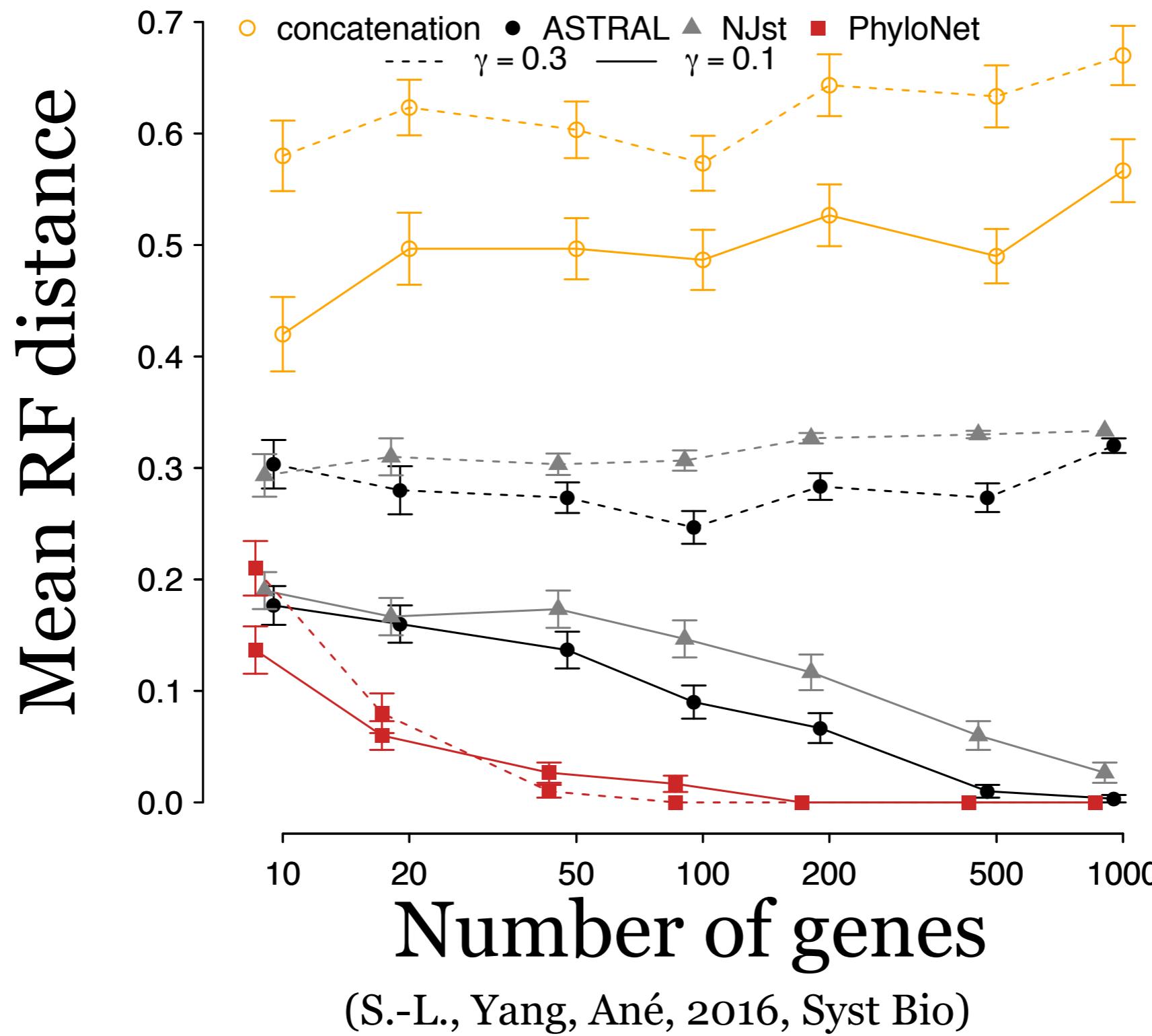
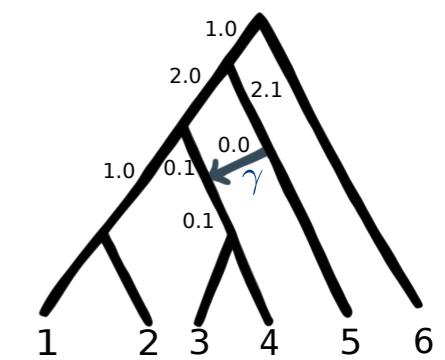
Anomaly zone with gene flow



(S.-L., Yang, Ané, 2016, Syst Bio)

Why? Phylogenetic network

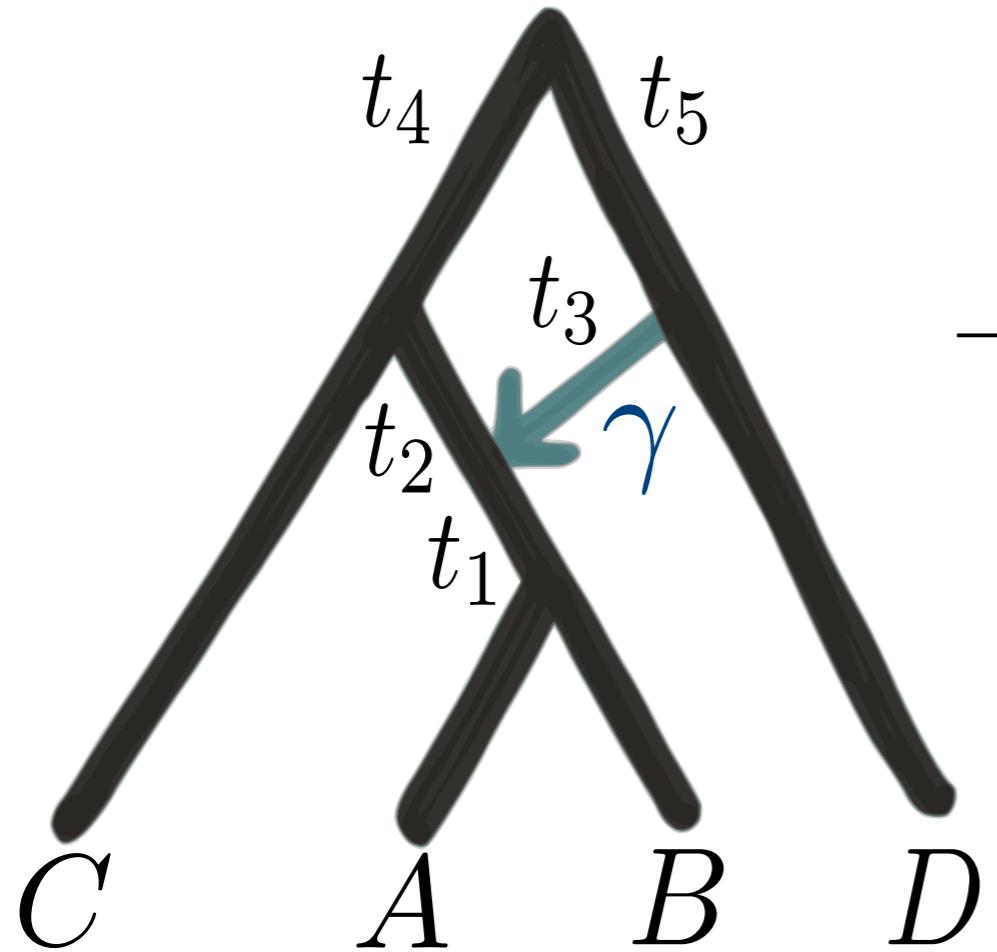
Coalescent tree methods
not robust to gene flow



Why?

Phylogenetic network

Anomalous unrooted
gene trees with gene flow



Frequency among gene trees

Quartet	$\gamma = 0.0$	$\gamma = 0.1$	$\gamma = 0.3$
$AB CD$	0.347	0.298	0.260
$CA BD$	0.327	0.351	0.370
$CB AD$	0.327	0.351	0.370

$$t_1 = t_2 = 0.01, t_3 = t_4 = t_5 = 1$$

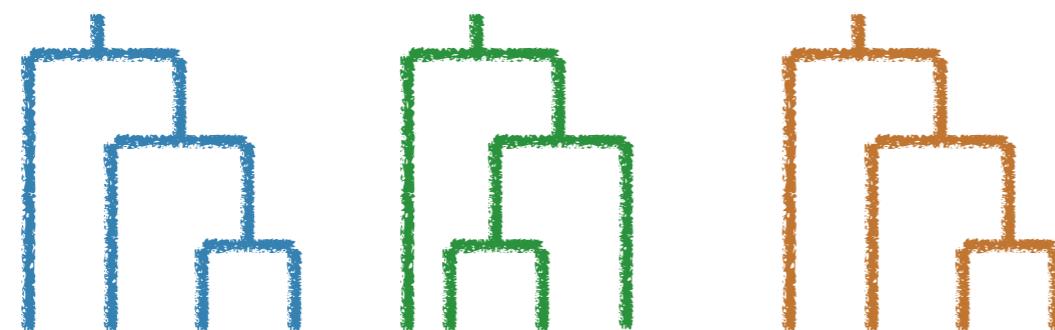
- **ILS**: no AUGT on 4 taxa (Degnan, 2013)
- **ILS+HGT**: AUGT on 4 taxa (S.-L., Yang, Ané, 2016, Syst Bio)

How?

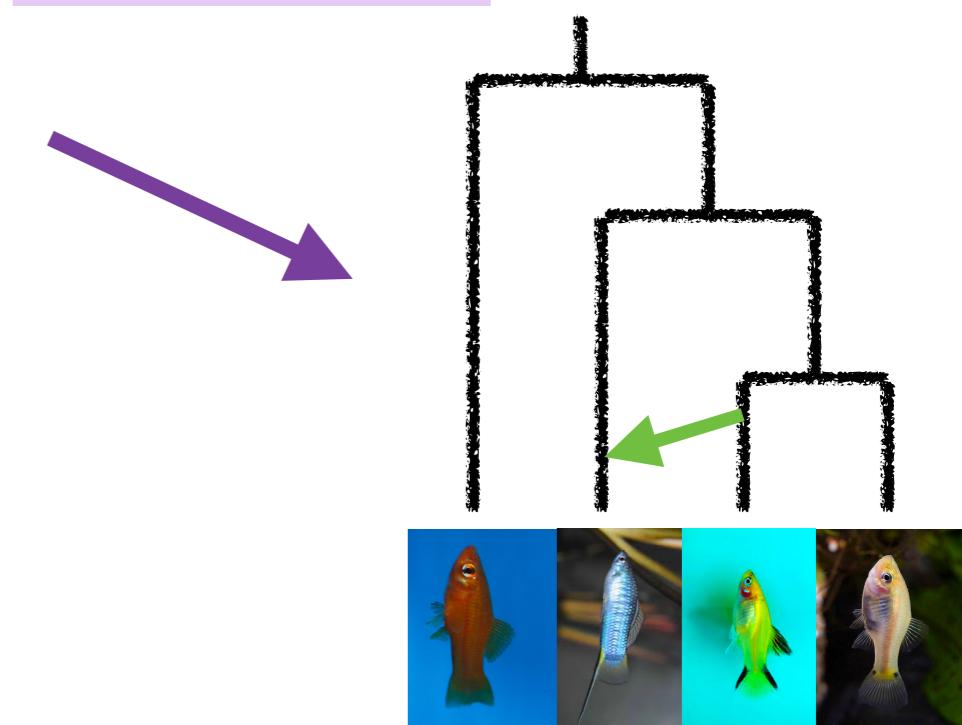
Phylogenetic network



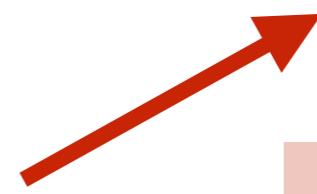
MrBayes
(Huelsenbeck, Ronquist, 2001)
RAxML
(Stamatakis, 2014)
PhyML
(Guindon et al, 2010)



BEAST2
(Zhang et al, 2017)
PhyloNet
(Wen et al, 2016)



SNaQ
(S.-L., Ane, 2016)
PhyloNet
(Yu et al, 2014)



Multispecies coalescent on a network



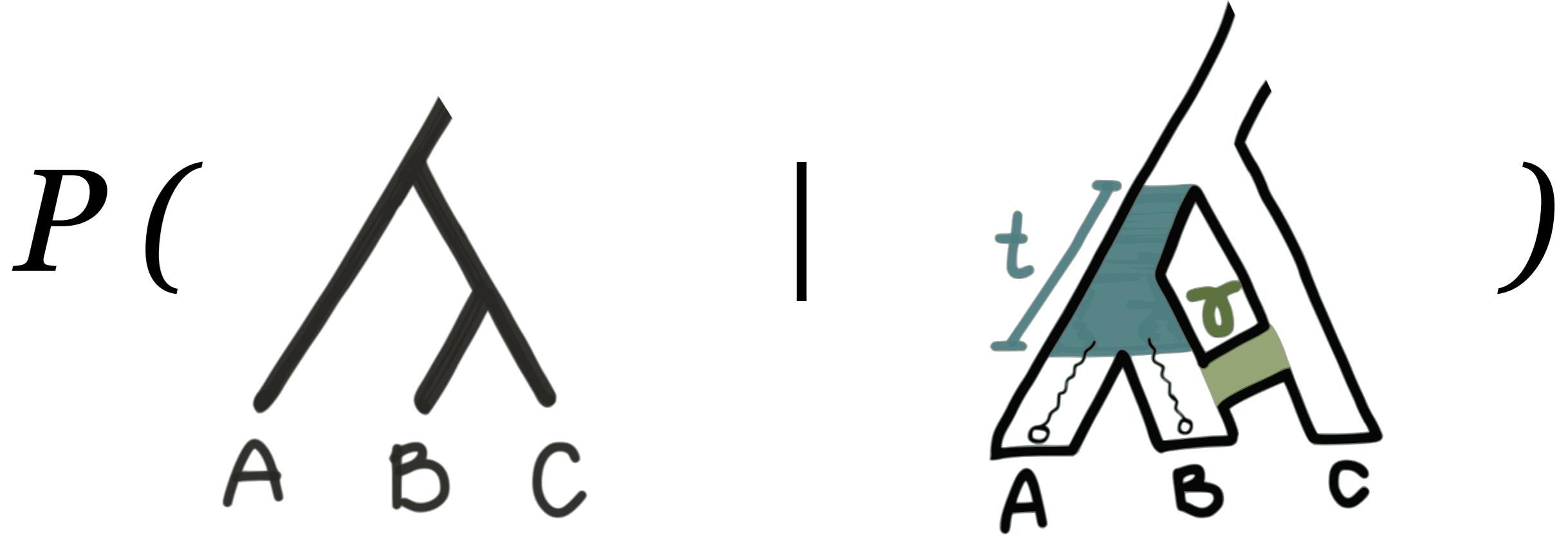
(Meng, Kubatko, 2009)
(Yu, Degnan, Nakhleh, 2012)

Multispecies coalescent on a network



(Meng, Kubatko, 2009)
(Yu, Degnan, Nakhleh, 2012)

Multispecies coalescent on a network



(Meng, Kubatko, 2009)
(Yu, Degnan, Nakhleh, 2012)



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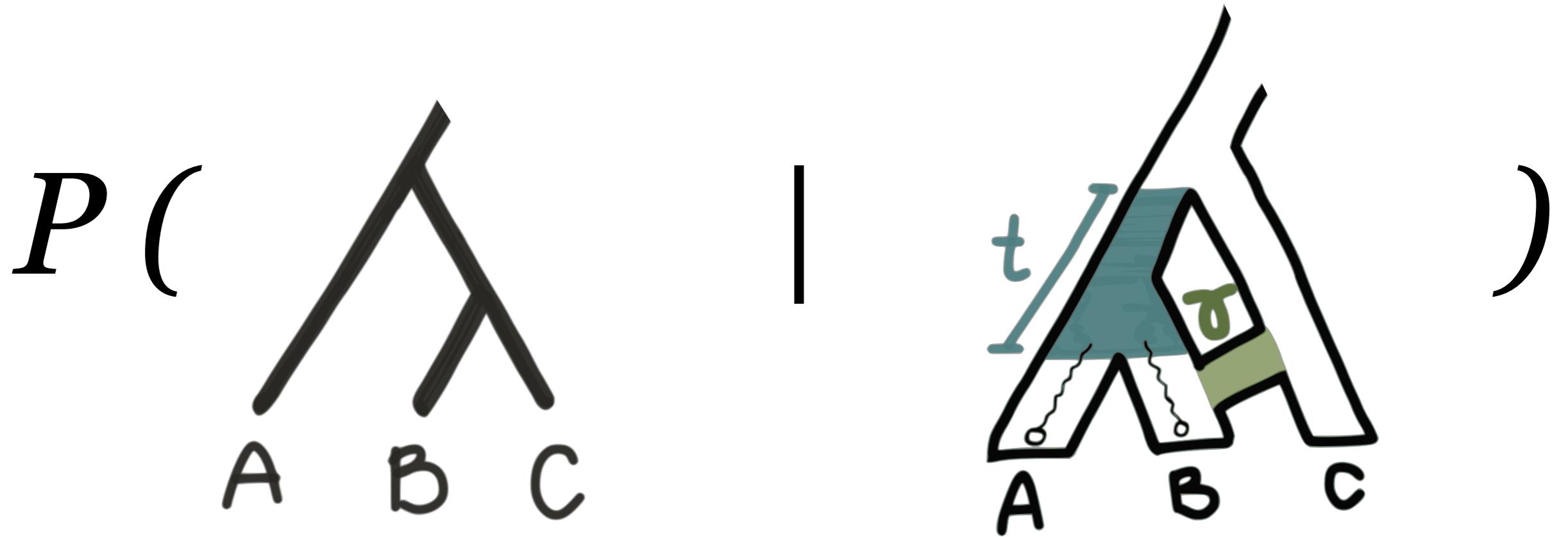


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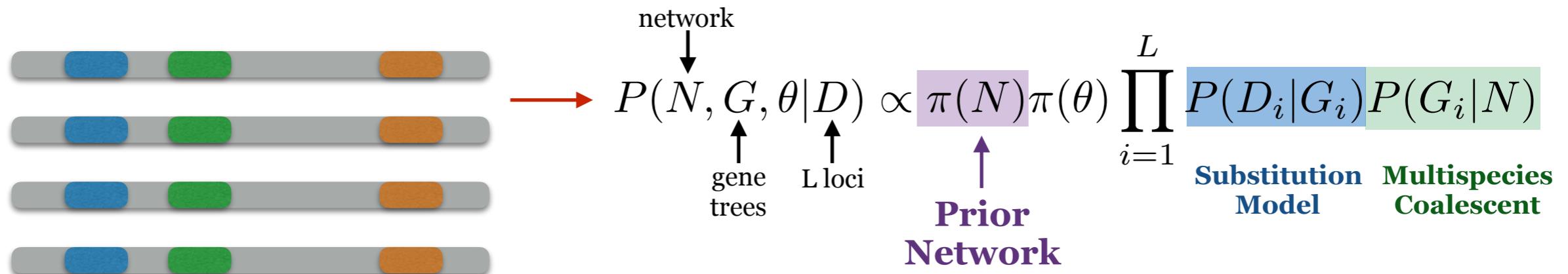
crsl4

Multispecies coalescent on a network



$$p_{BC|AD}(t, t_2, \gamma) = (1 - \gamma) \frac{1}{3} e^{-t} + \gamma (1 - \frac{2}{3} e^{-t_2})$$

(Meng, Kubatko, 2009)
(Yu, Degnan, Nakhleh, 2012)

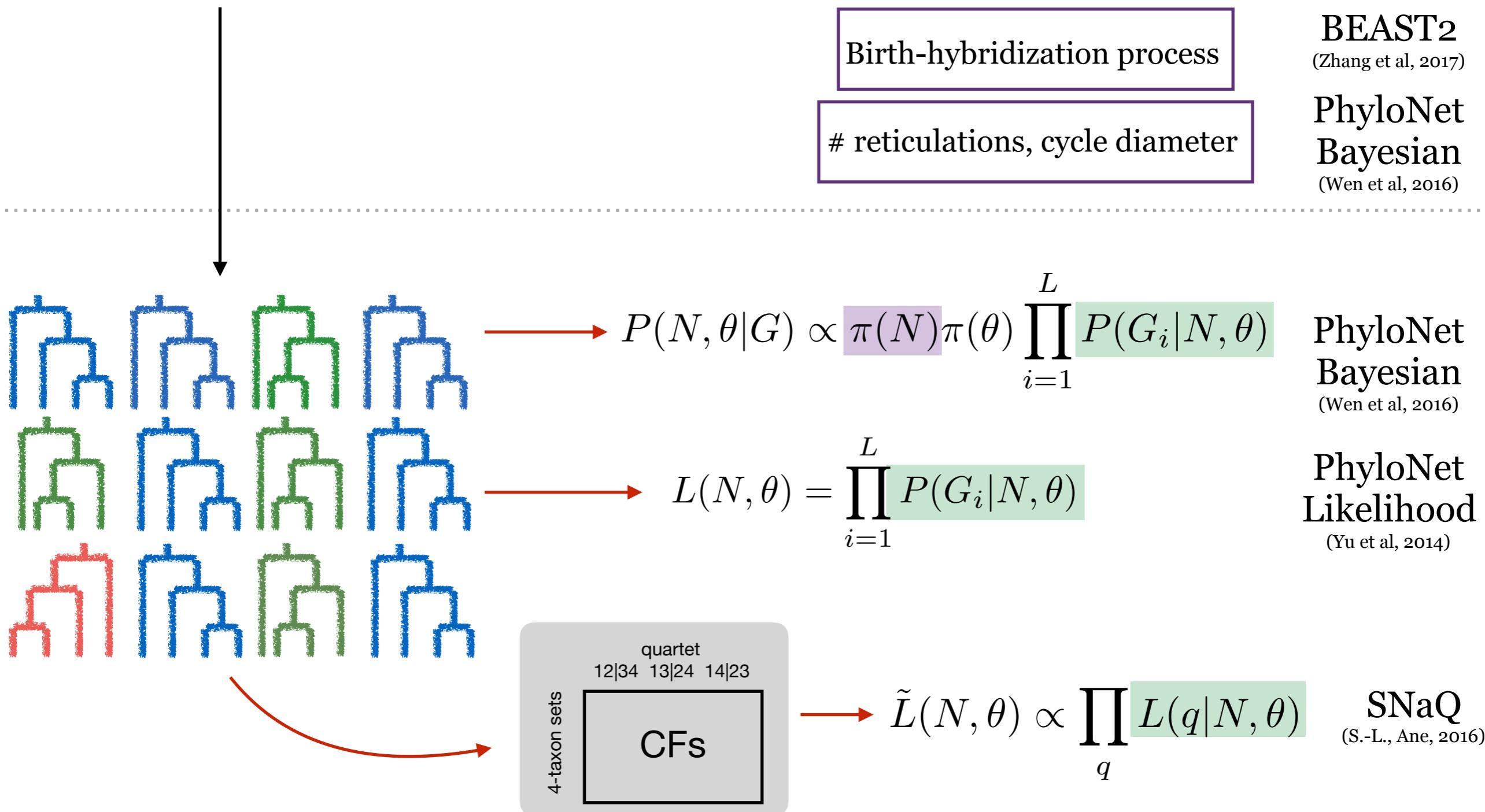
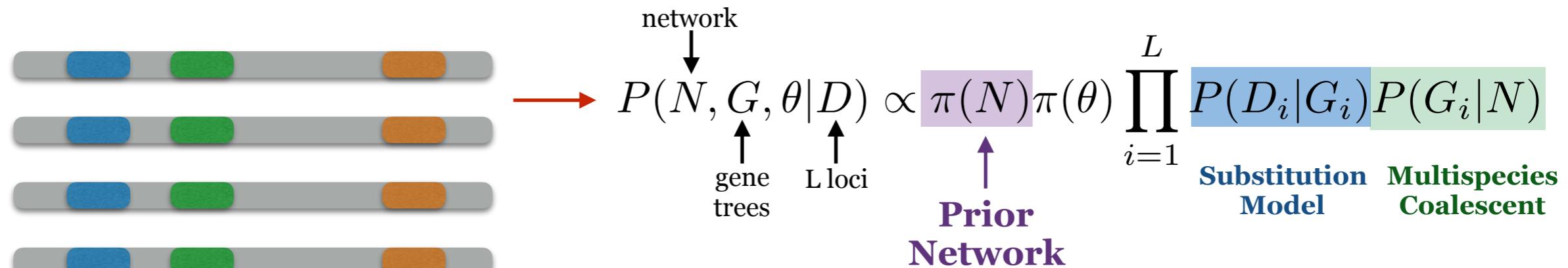


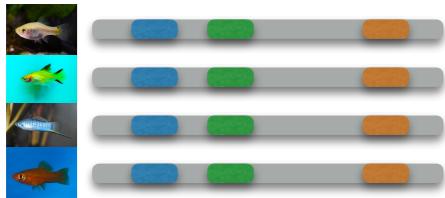
Birth-hybridization process

reticulations, cycle diameter

BEAST2
(Zhang et al, 2017)

PhyloNet Bayesian
(Wen et al, 2016)

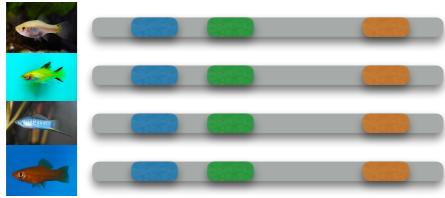




BEAST2
(Zhang et al, 2017)

Birth-hybridization process

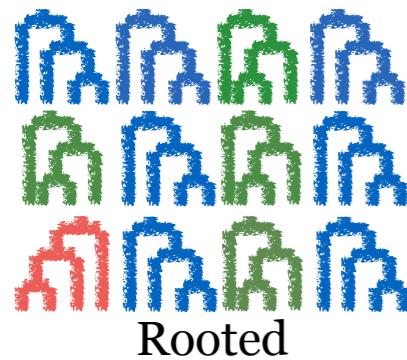
Most accurate,
not scalable



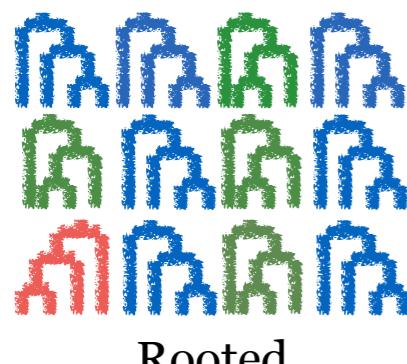
PhyloNet
Bayesian
(Wen et al, 2016)

MCMC:
Network moves,
mixing

reticulations,
cycle diameter

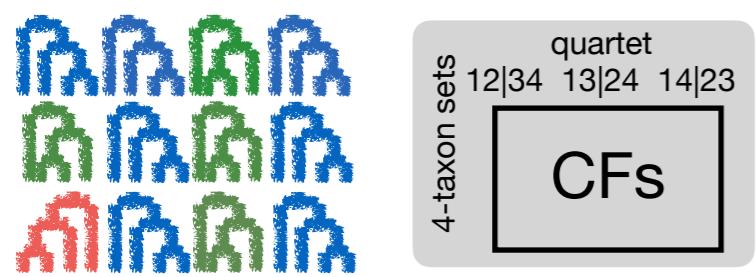


PhyloNet
Bayesian
(Wen et al, 2016)



PhyloNet
Likelihood
(Yu et al, 2014)

Heuristic search:
Network moves



SNaQ
(S.-L., Ane, 2016)

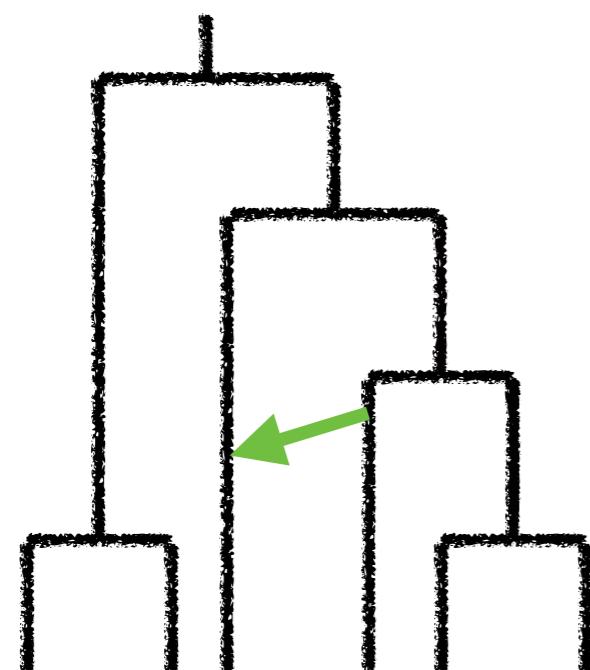
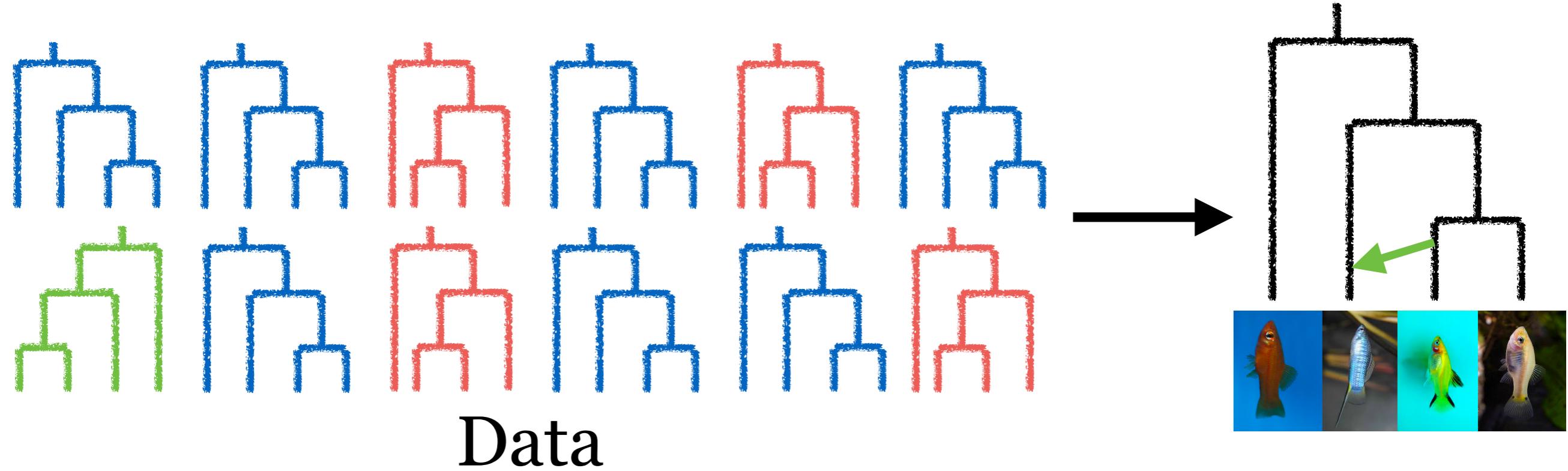
Level-1
networks

More scalable,
Robust

Unrooted

STEM-hy	gene trees rooted, BL	likelihood	hybridization b/w sister lineages
PhyloNet InferNetwork_ML	gene trees rooted	likelihood	
PhyloNet InferNetwork_MPL	gene trees rooted	triplet likelihood	
Phylogenetworks SNaQ	gene trees or quartet CFs	quartet likelihood	level-1 network
PhyloNet MCMC_GT	gene trees rooted	Bayesian	compound prior
PhyloNet MCMC_SEQ	alignments	Bayesian	compound prior no rate variation
BEAST2 SpeciesNetwork	alignments	Bayesian	birth-hyb prior
PhyloNet MLE_BiMarkers	biallelic sites	likelihood	compound prior
PhyloNet MCMC_BiMarkers	biallelic sites	Bayesian	compound prior
HyDe	sites	invariants	4 taxa, 1 hyb.

Maximum pseudolikelihood



Quartet-based inference

$$\tilde{L}(\textit{network}) = \prod L(\textit{quartet})$$

(S-L, Ané, 2016, PLoS Genetics)

www.github.com/CRSL4/PhyloNetworks

snaQ julia



<https://solislemuslab.github.io/>

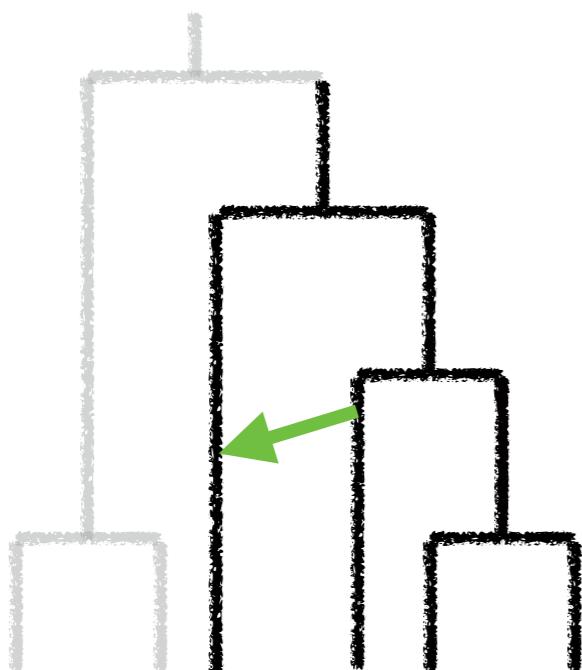
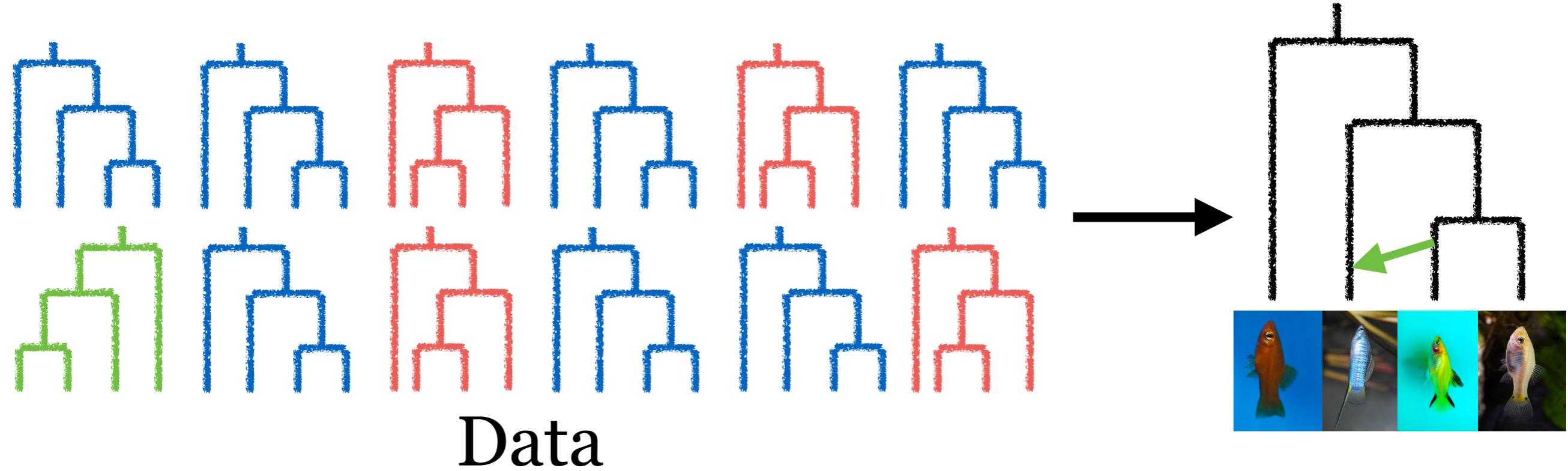


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Maximum pseudolikelihood



Quartet-based inference

$$\tilde{L}(\textit{network}) = \prod L(\textit{quartet})$$

(S-L, Ané, 2016, PLoS Genetics)

[www.github.com/CRSL4/PhyloNetworks](https://github.com/CRSL4/PhyloNetworks)

snaQ julia



<https://solislemuslab.github.io/>

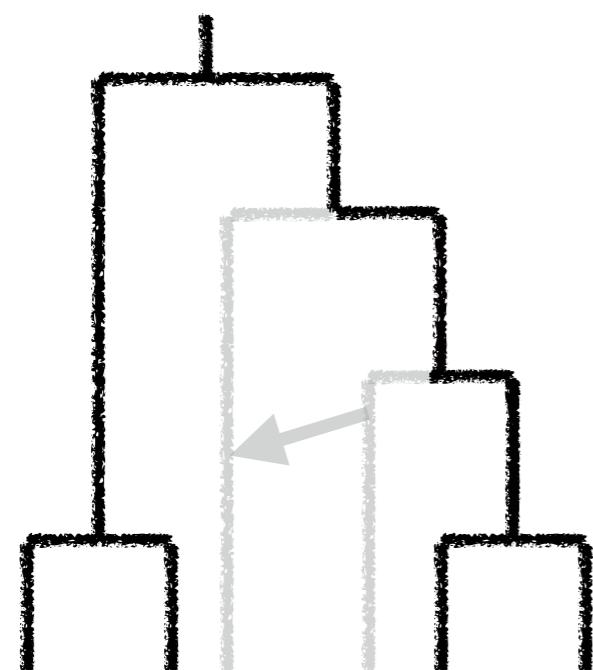
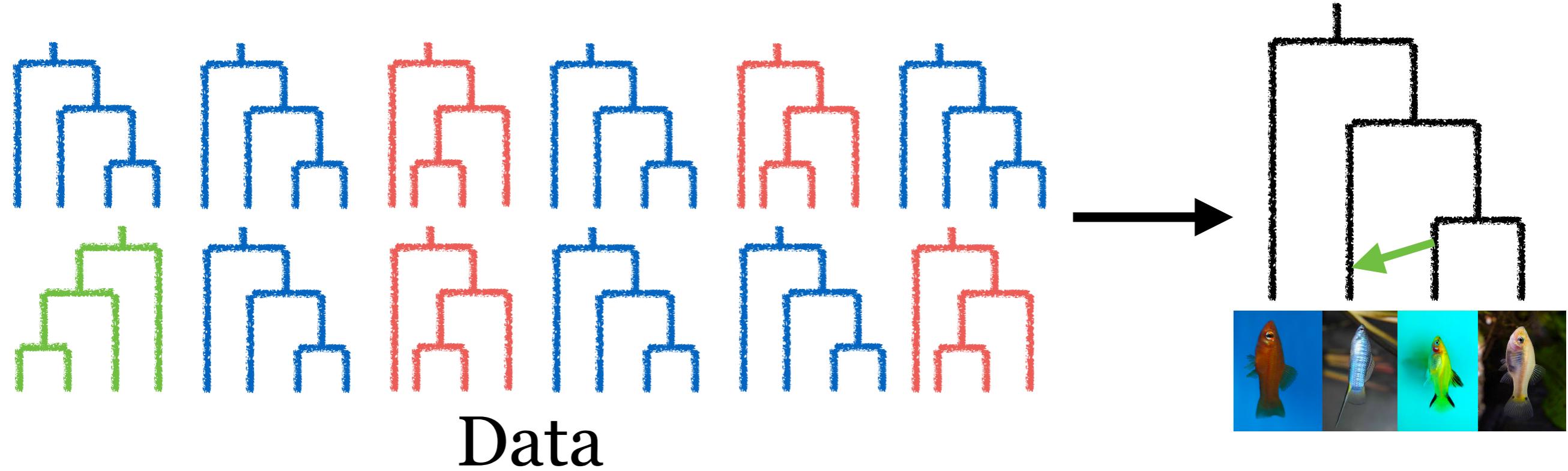


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Maximum pseudolikelihood



Quartet-based inference

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[www.github.com/CRSL4/PhyloNetworks](https://github.com/CRSL4/PhyloNetworks)

snaQ julia



<https://solislemuslab.github.io/>



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Maximum pseudolikelihood

Unrooted gene trees

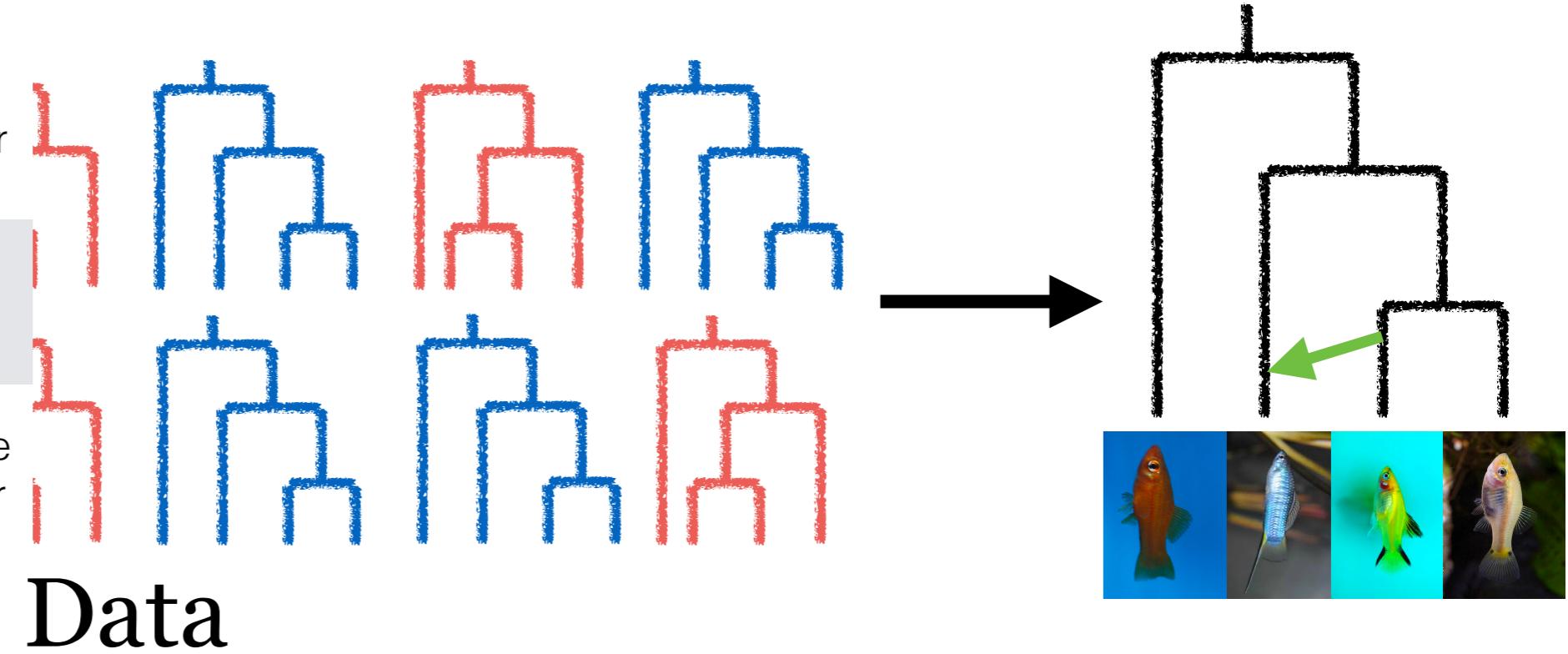
No branch lengths

Concordance factors

No rooting error

No molecular clock assumption

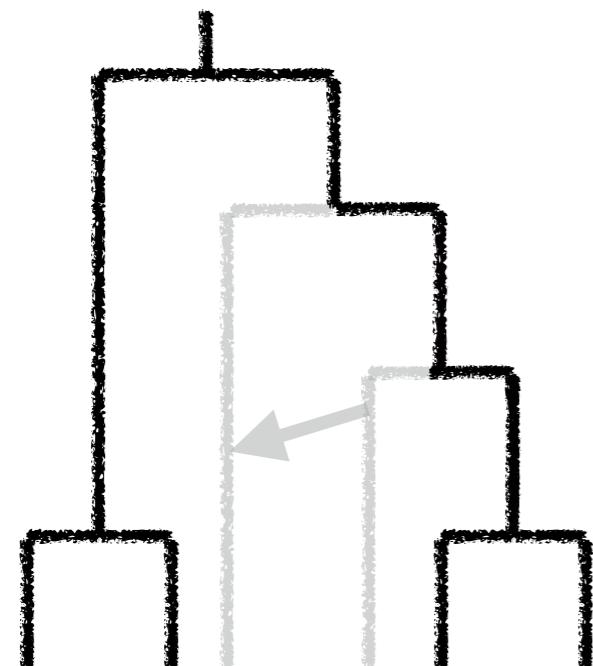
Account for tree estimation error



$$\tilde{L}(\textit{network}) = \prod L(\textit{quartet})$$

(S-L, Ané, 2016, PLoS Genetics)

[www.github.com/CRSL4/PhyloNetworks](https://github.com/CRSL4/PhyloNetworks)



Quartet-based inference

snaQ julia



<https://solislemuslab.github.io/>

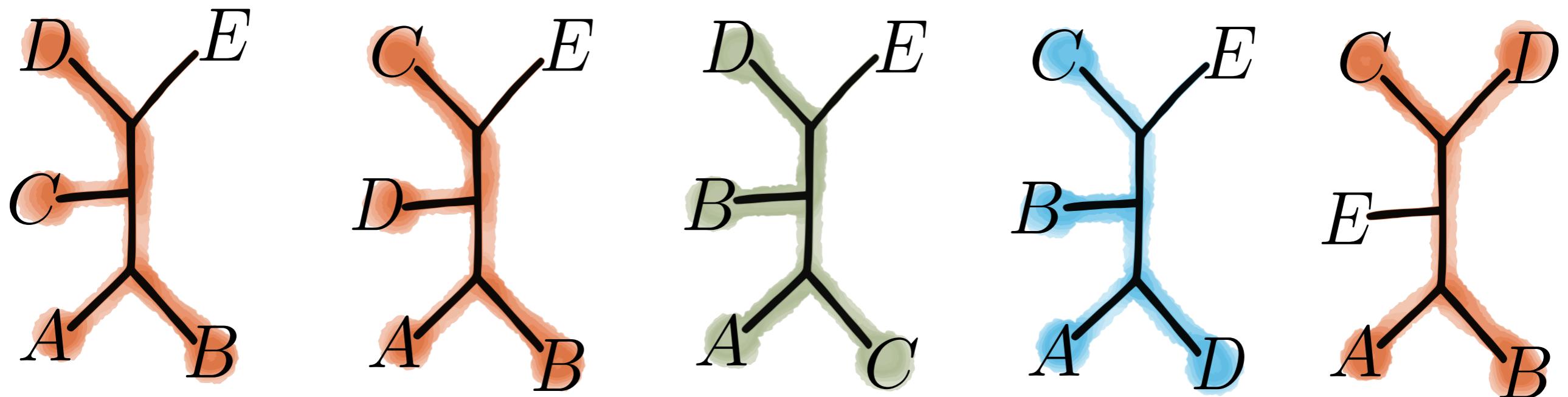


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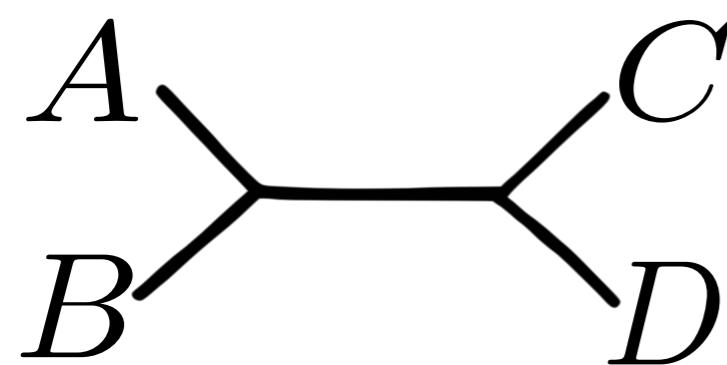


crsl4

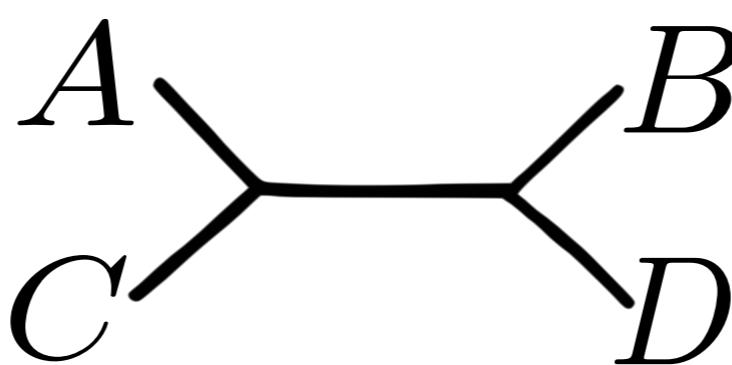
Quartet-based inference



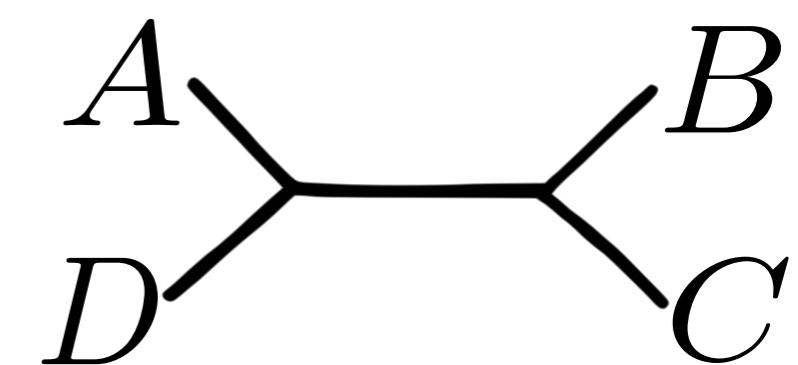
Concordance factors (CF):
% of genes having the quartet in their tree



3/5



1/5



1/5



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Quartet-based inference

Observed **quartet** CFs:

4 taxon set	CF_1	CF_2	CF_3
A B C D	.80	.10	.10
A B C E	.40	.40	.20
A B D E	.40	.40	.20
A C D E	.84	.08	.08
B C D E	.82	.10	.08

inferred network:

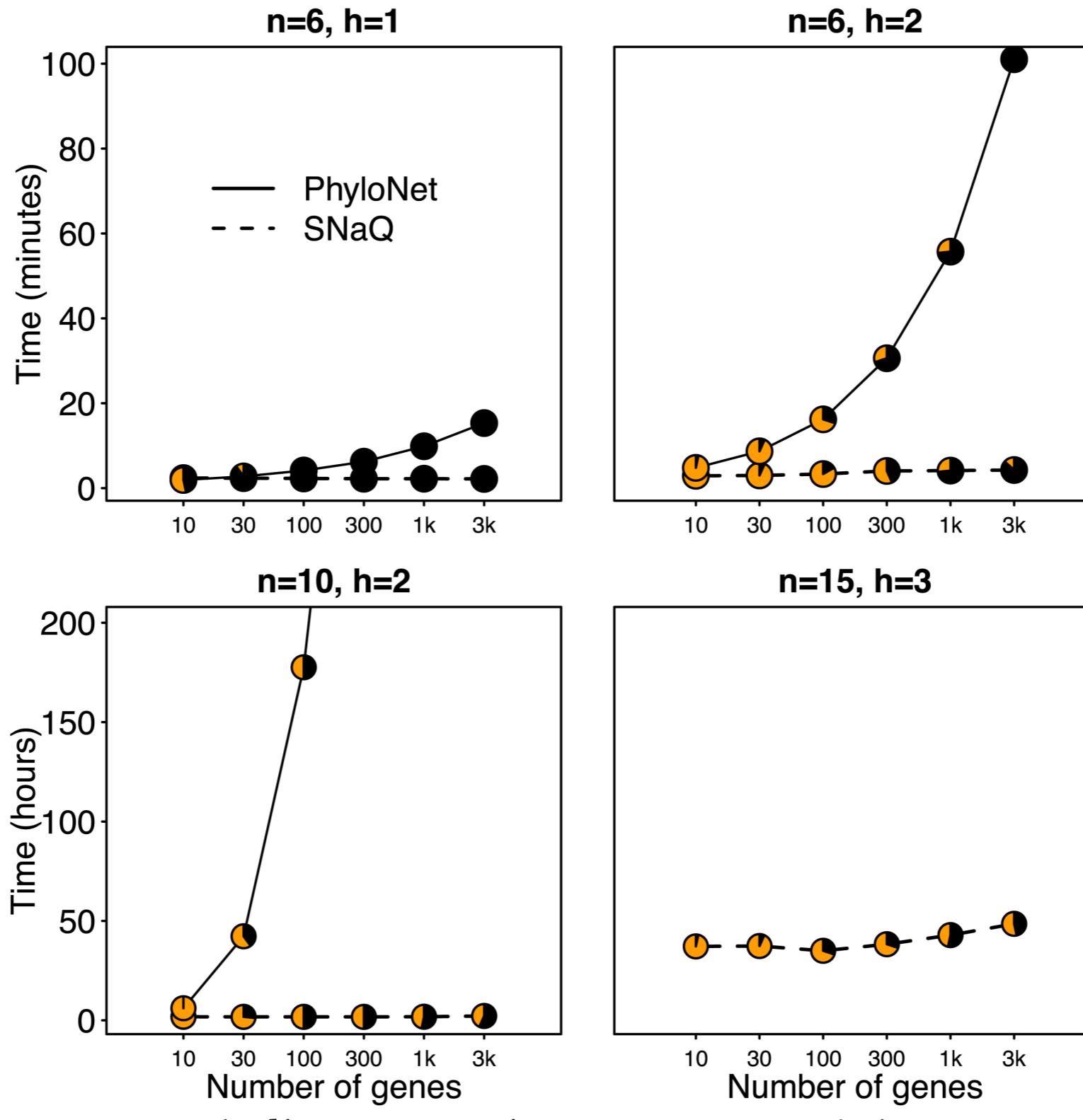


Maximum Pseudo-Likelihood:

$$\log \tilde{L} = \sum_{q \in Q(N)} CF_{in,1} \log(CF_{net,1}) + CF_{in,2} \log(CF_{net,2}) + CF_{in,3} \log(CF_{net,3})$$



Scalability gains



(Solís-Lemus, Ané, 2016, PLoS Genetics)



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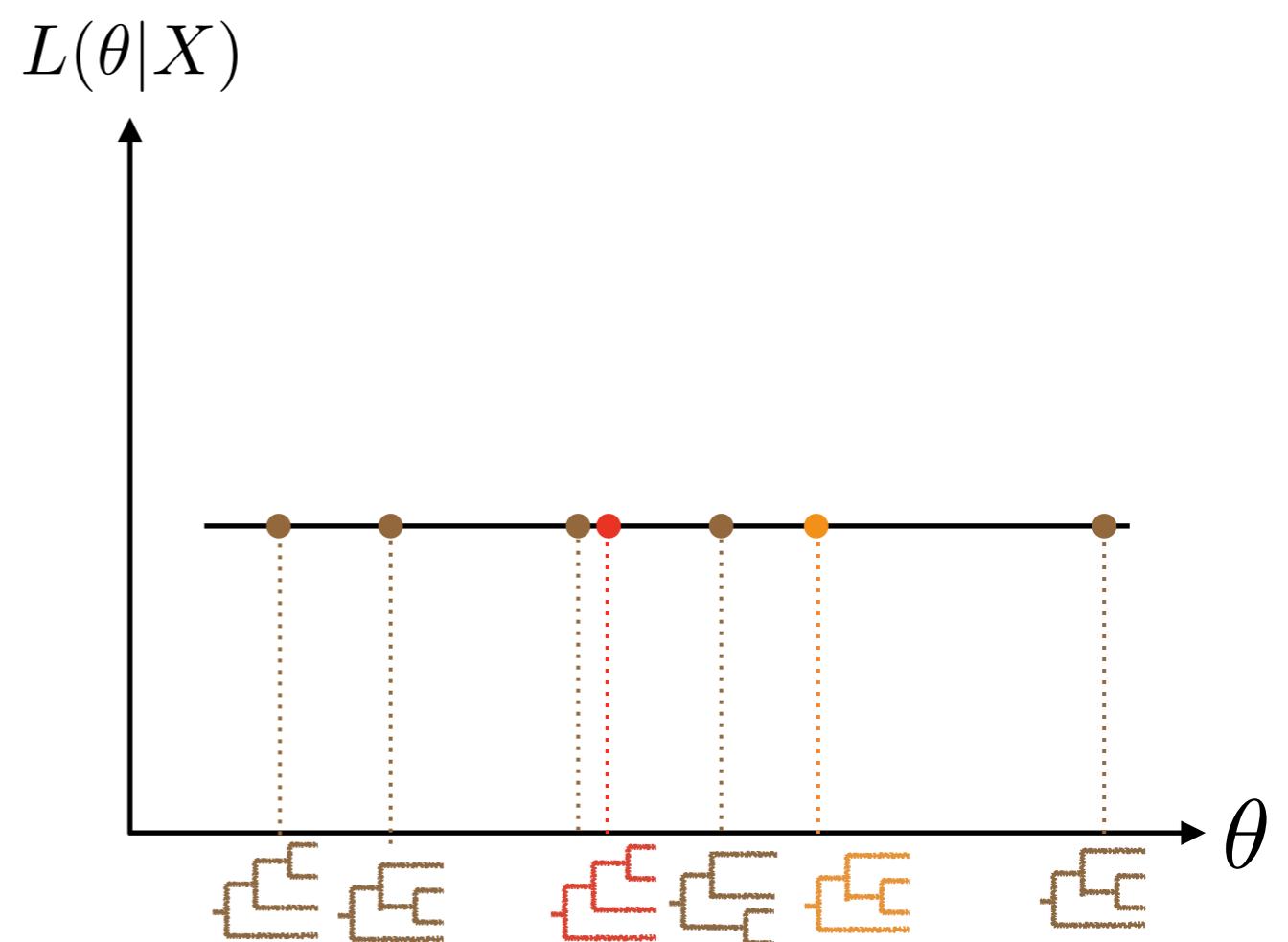
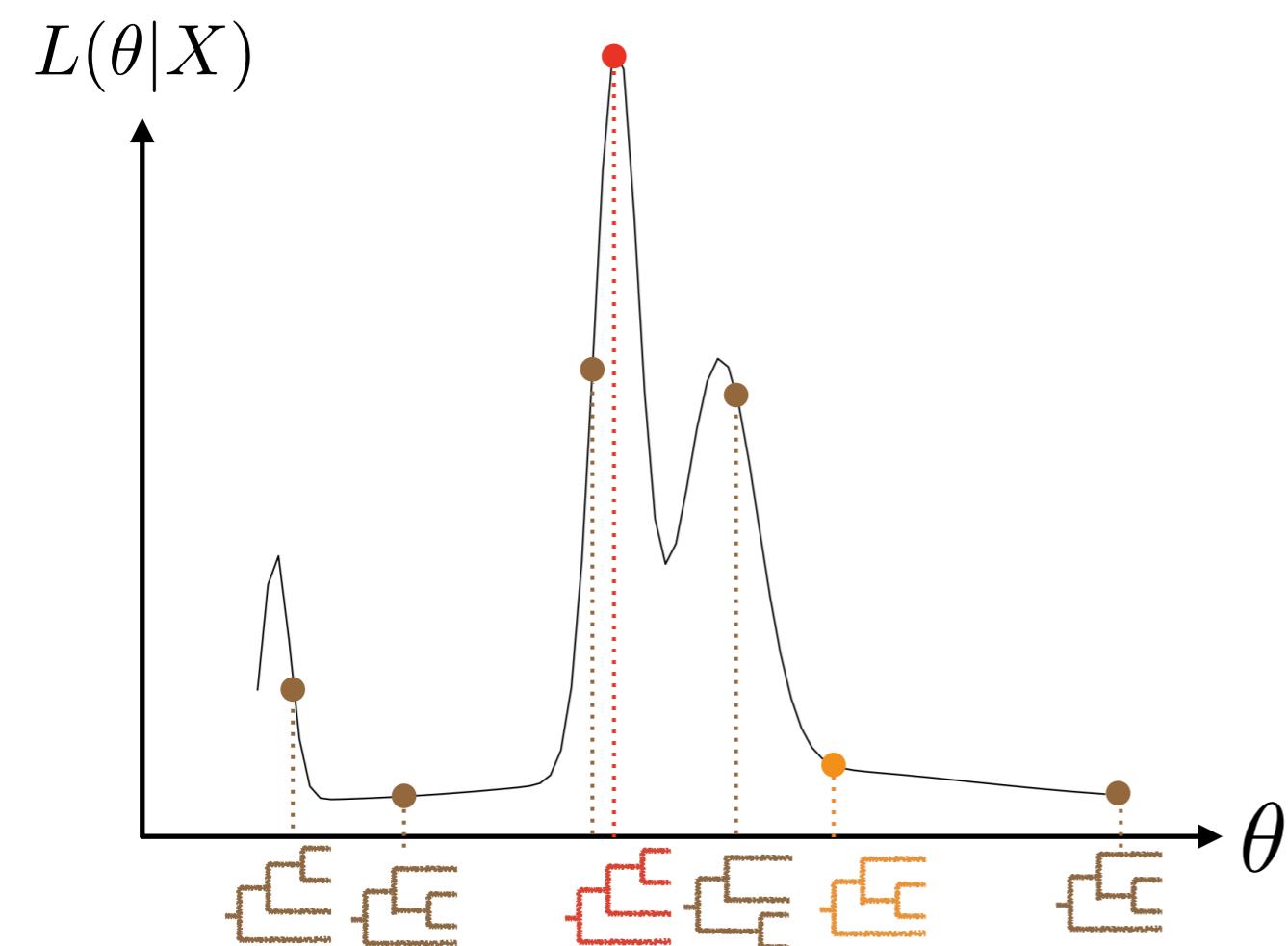


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Challenges

- Network space
- Identifiability
- Network comparison

Identifiability

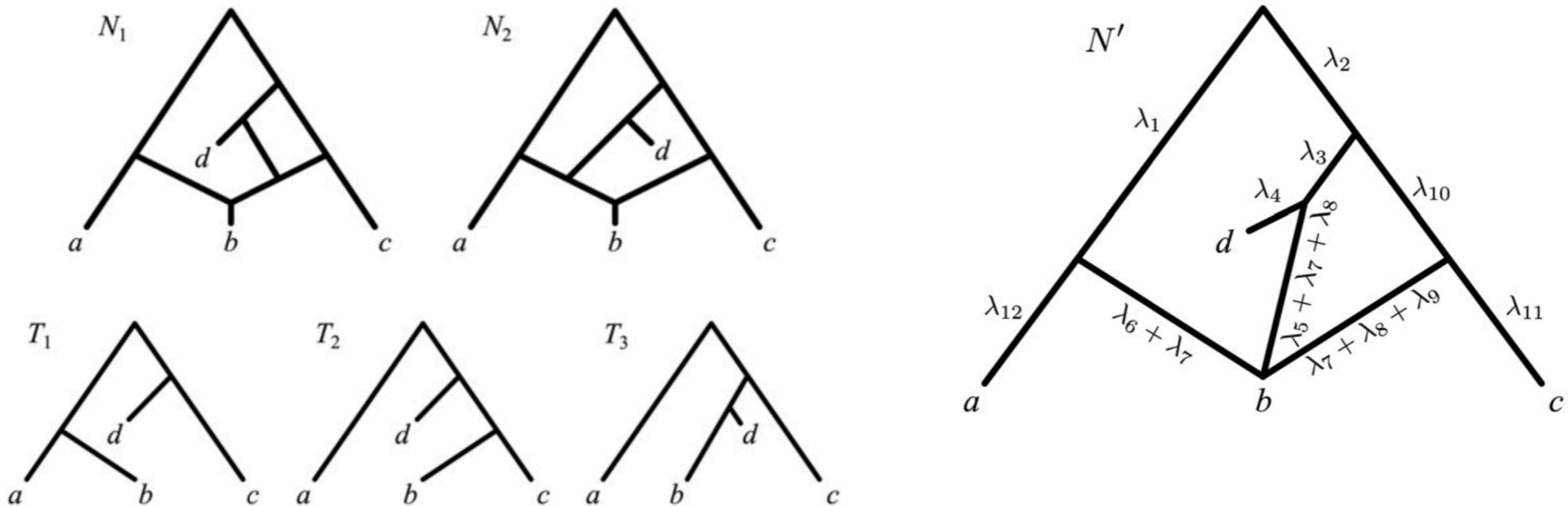


RESEARCH ARTICLE

Reconstructible Phylogenetic Networks: Do Not Distinguish the Indistinguishable

Fabio Pardi^{1,3*}, Celine Scornavacca^{2,3}

1 Laboratoire d’Informatique, de Robotique et de Microélectronique de Montpellier (LIRMM, UMR 5506) CNRS, Université de Montpellier, France, **2** Institut des Sciences de l’Evolution de Montpellier (ISE-M, UMR 5554) CNRS, IRD, Université de Montpellier, France, **3** Institut de Biologie Computationnelle, Montpellier, France

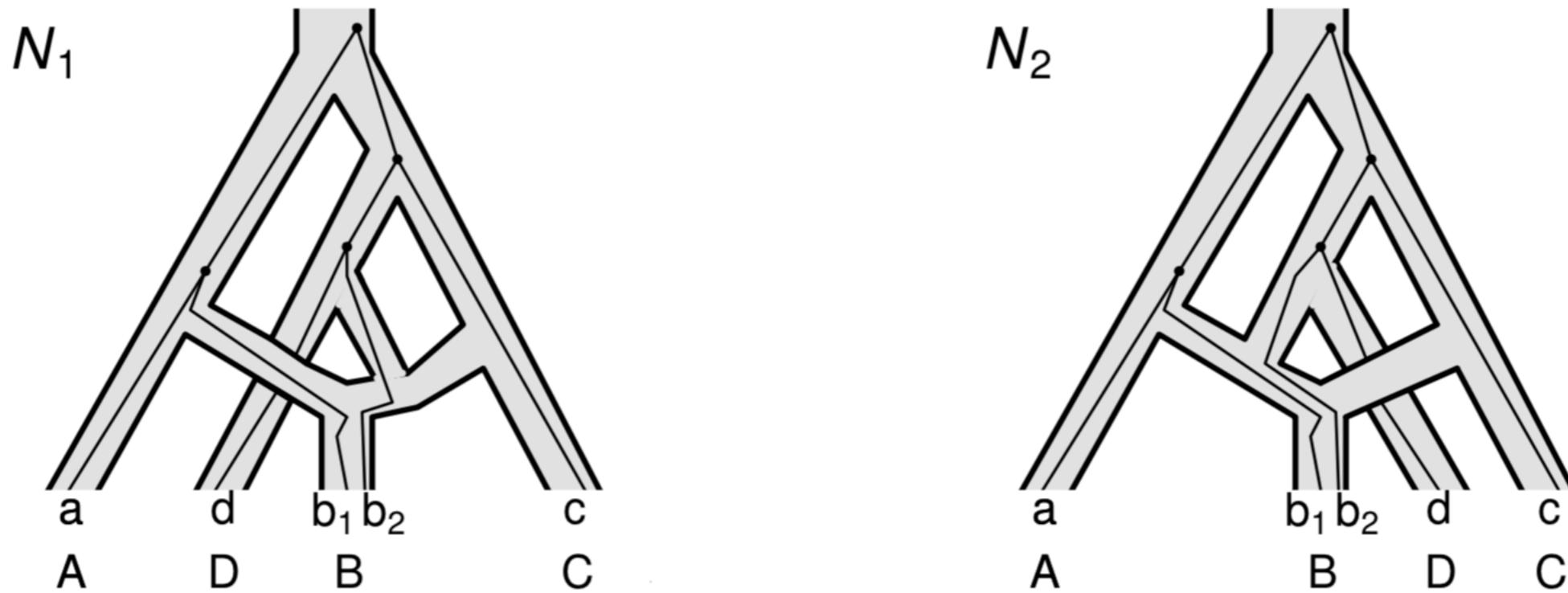


Undistinguishable with the
“displayed trees” criterion

Solution: Canonical
network (“unzipped”)

Displayed Trees Do Not Determine Distinguishability Under the Network Multispecies Coalescent

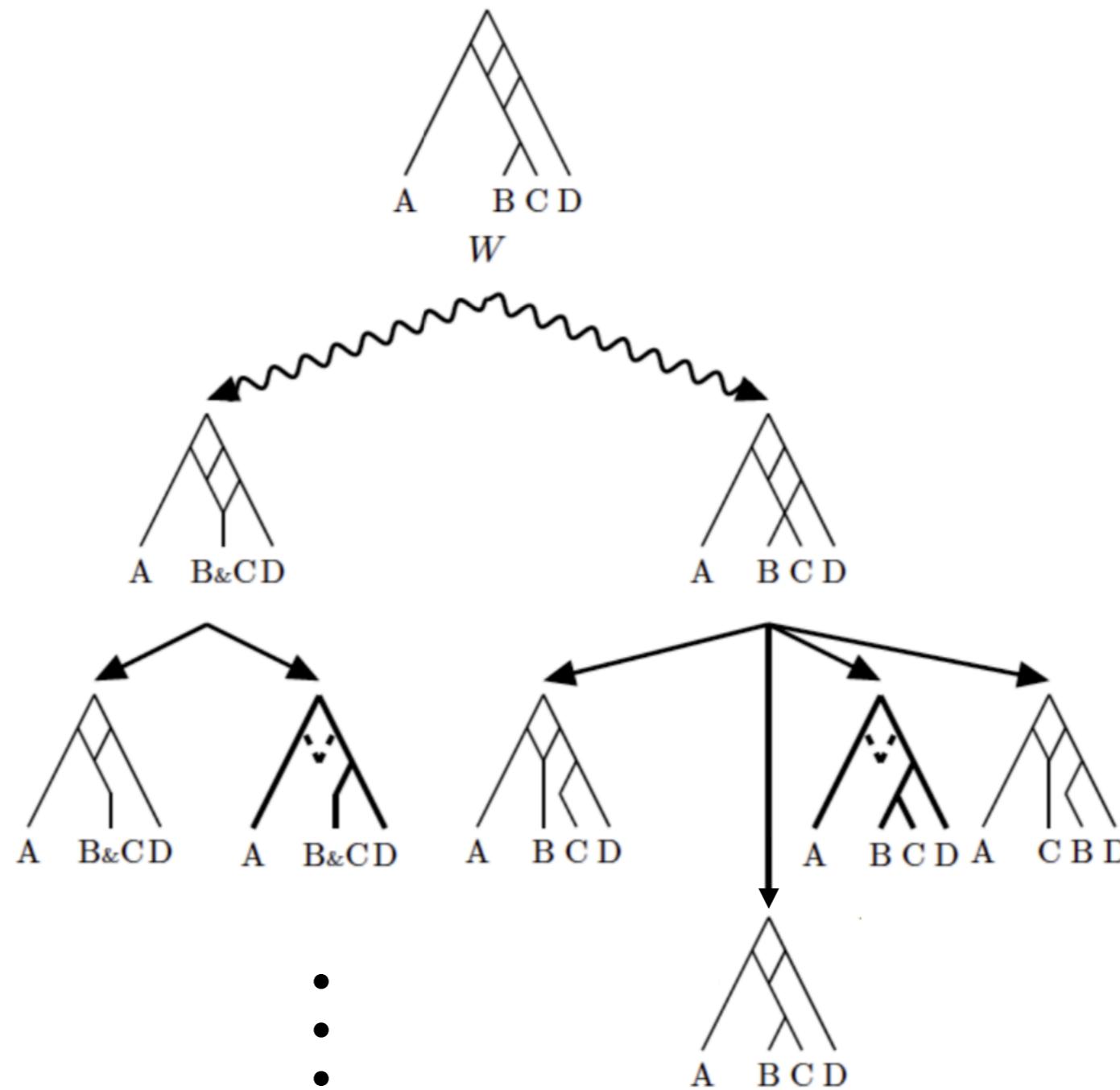
Sha Zhu¹, James H. Degnan²



Distinguishable under the MSC

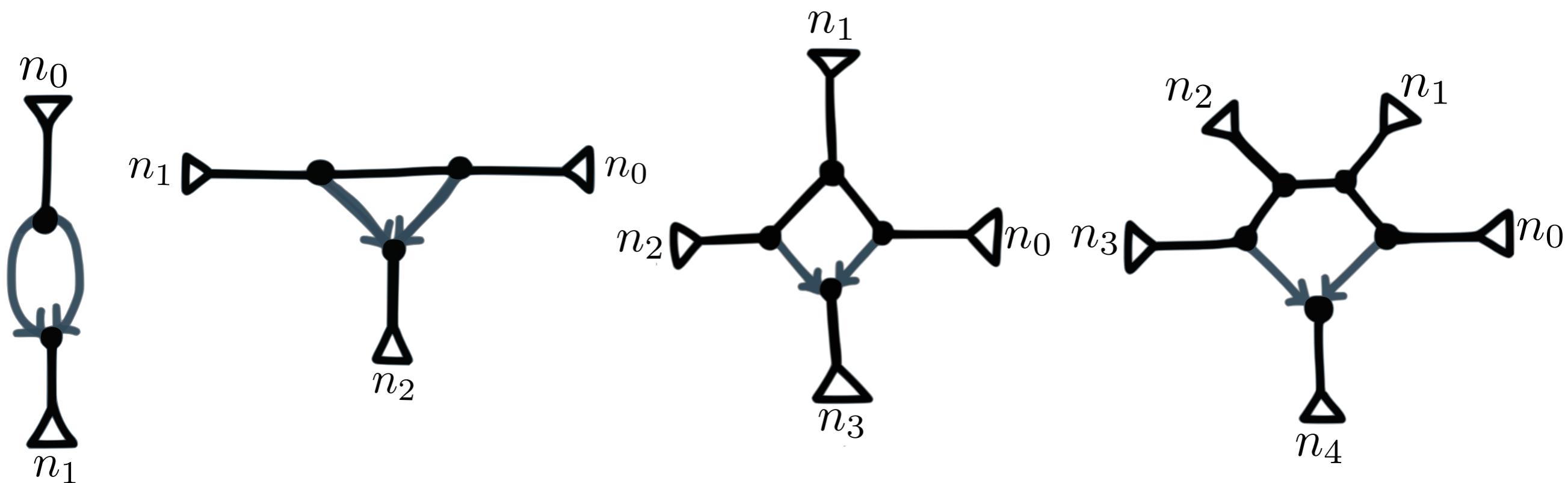
Displayed Trees Do Not Determine Distinguishability Under the Network Multispecies Coalescent

Sha Zhu¹, James H. Degnan²



Decomposing network in **parental** trees

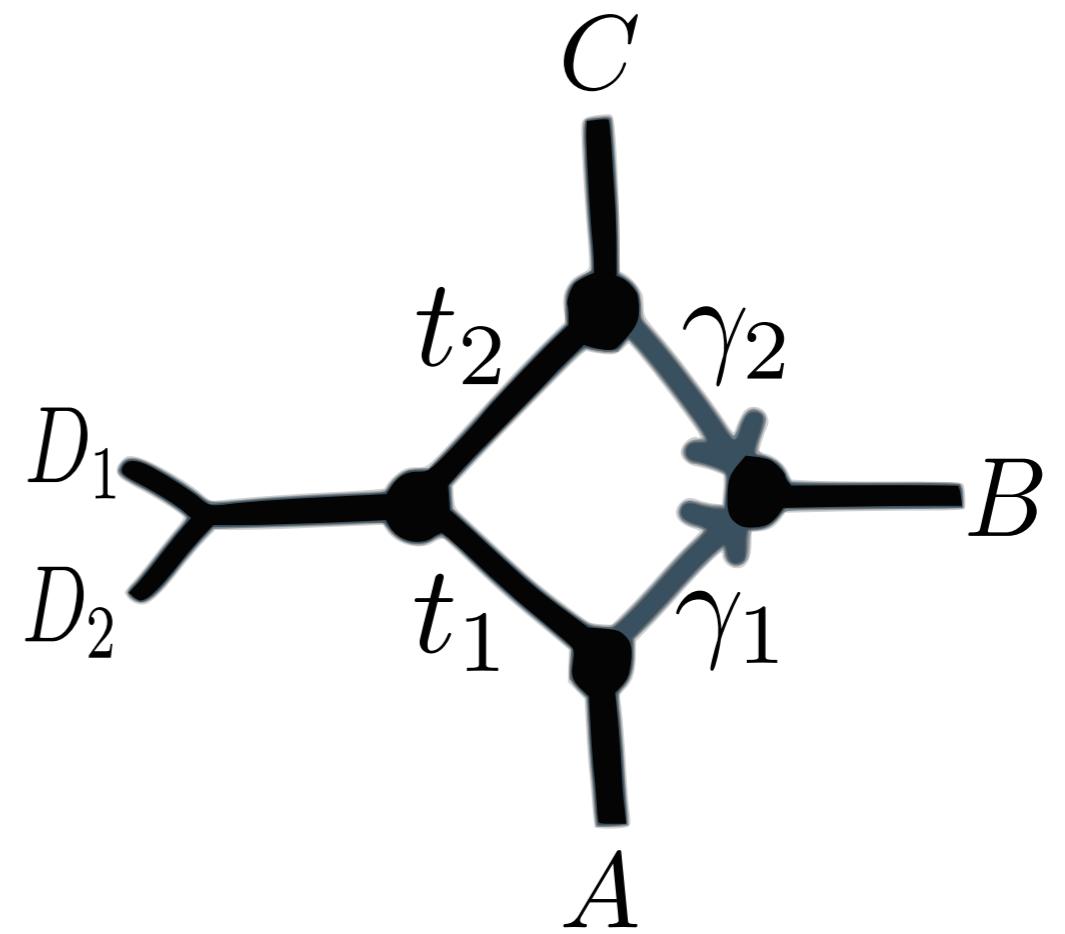
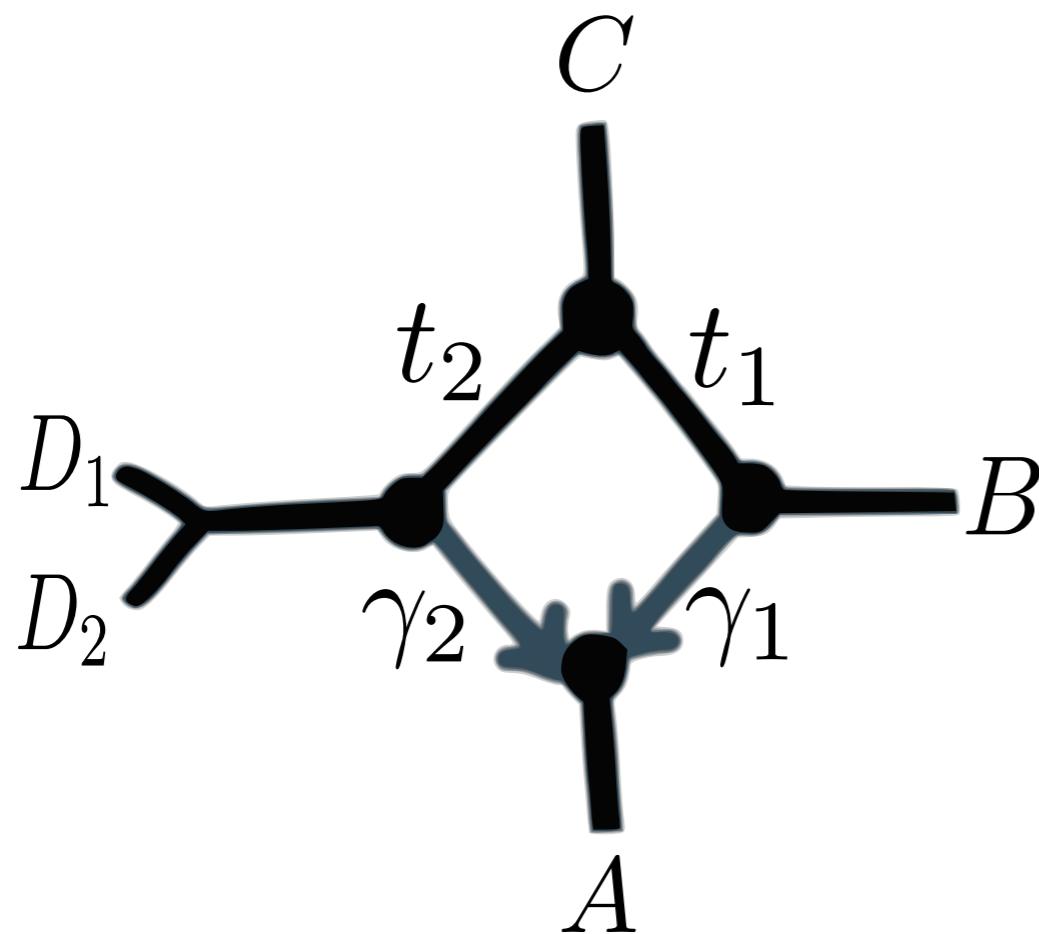
RESEARCH ARTICLE

Inferring Phylogenetic Networks with
Maximum Pseudolikelihood under
Incomplete Lineage SortingClaudia Solís-Lemus^{1*}, Cécile Ané^{1,2}Can we detect the
presence of
hybridization in level-1
networks?**No****Yes**
 $(n_i, n_j \geq 2)$ **Yes**
 $(n_i \geq 2)$ **Yes**

Generic Identifiability

 $t_i \in (0, \infty), \gamma \in (0, 1)$

In practice: flat pseudolikelihood

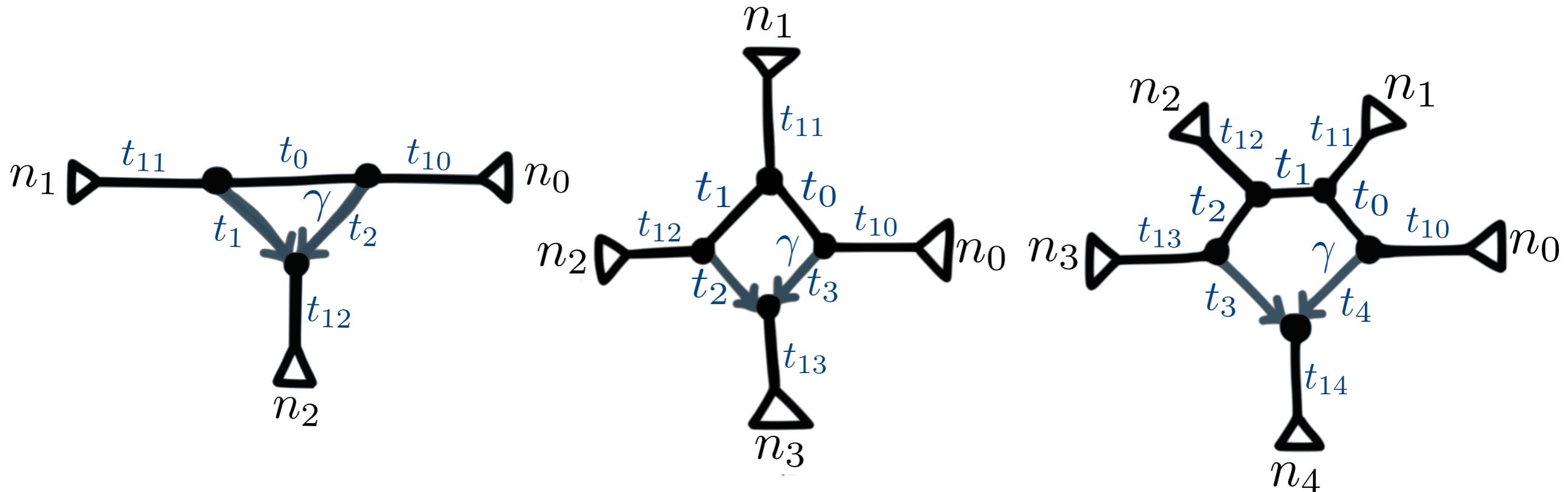


Can we estimate numerical parameters?

RESEARCH ARTICLE

Inferring Phylogenetic Networks with Maximum Pseudolikelihood under Incomplete Lineage Sorting

Claudia Solís-Lemus^{1*}, Cécile Ané^{1,2}



No

Good triangle
($t_{12} = 0$)

Yes

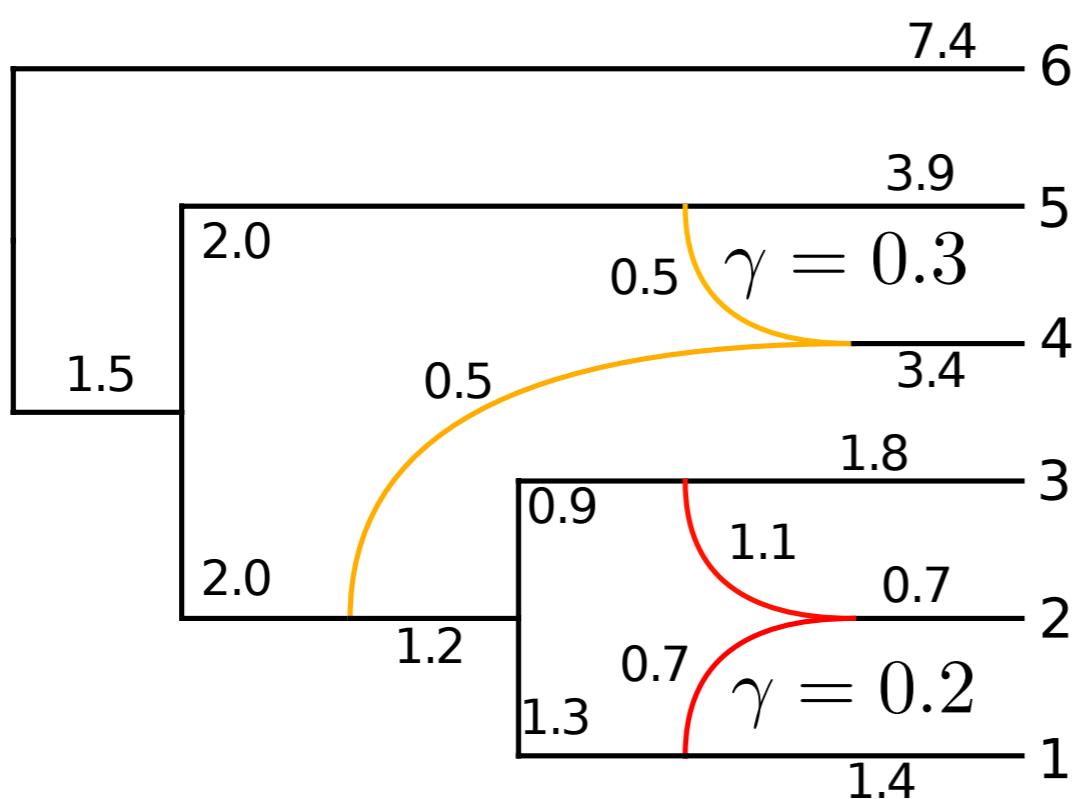
Good diamond
($n_0, n_2 \geq 2$)

Generic Identifiability

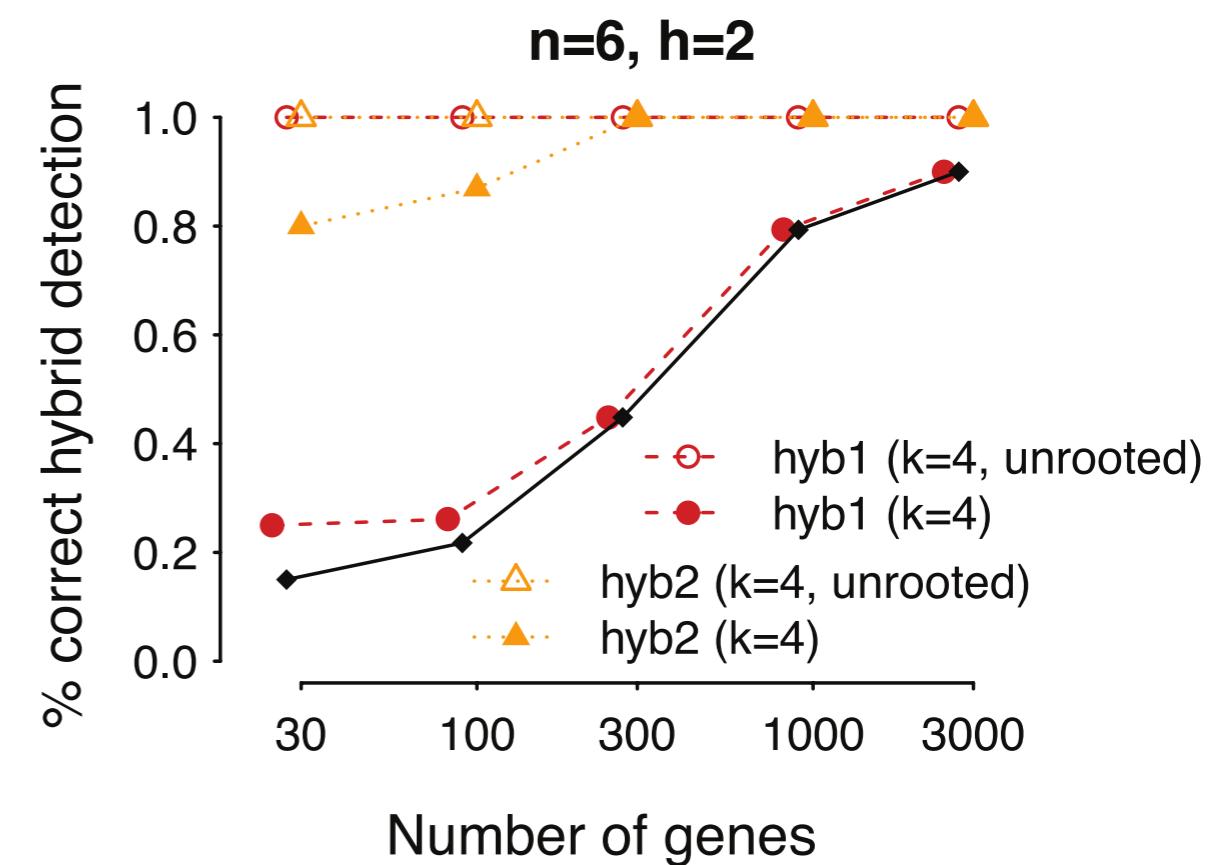
$t_i \in (0, \infty), \gamma \in (0, 1)$

Identifiability matters: SNaQ performance

Good diamond



Bad diamond



Challenges

- Network space

- Identifiability

Displayed vs Parental trees
Level-1 semi-directed networks
Hybridizations: case by case
Missing: likelihood, level-k semi-directed

- Network comparison

Challenges

- Network space

K. Huber, V. Moulton, C. Scornavacca,...
Missing: path through tree space, semi-directed

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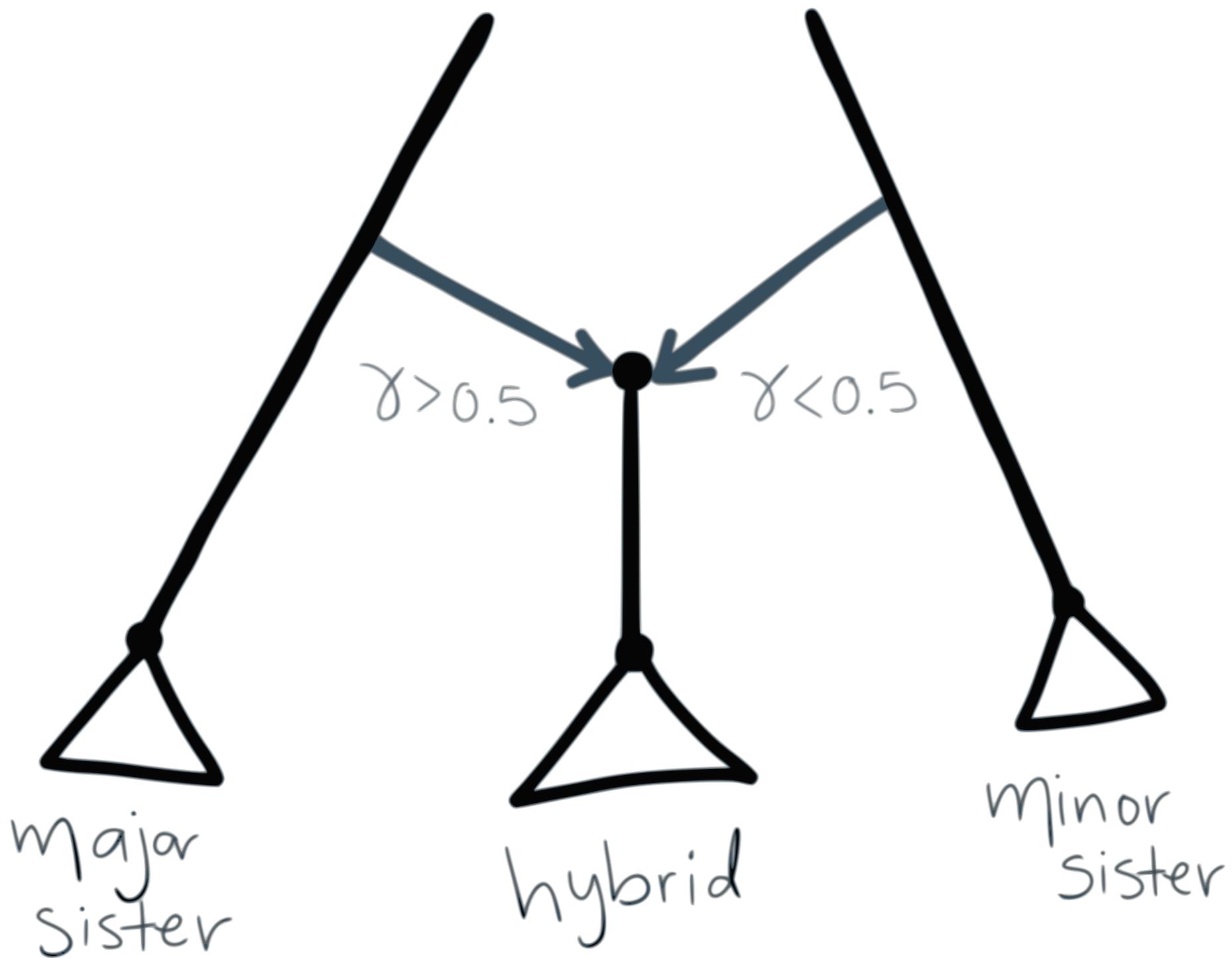
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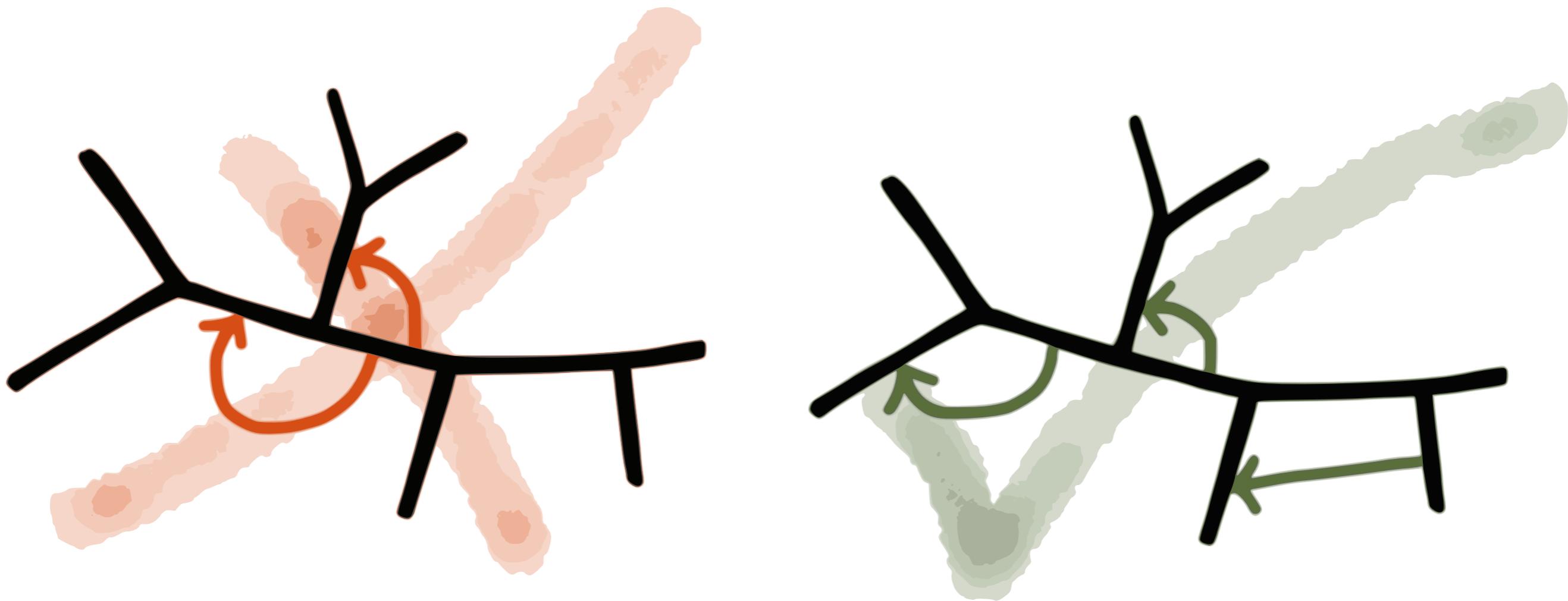

Missing: distance function
Hardwired-cluster distance only for rooted networks
Summary of networks: clades!

Network summary



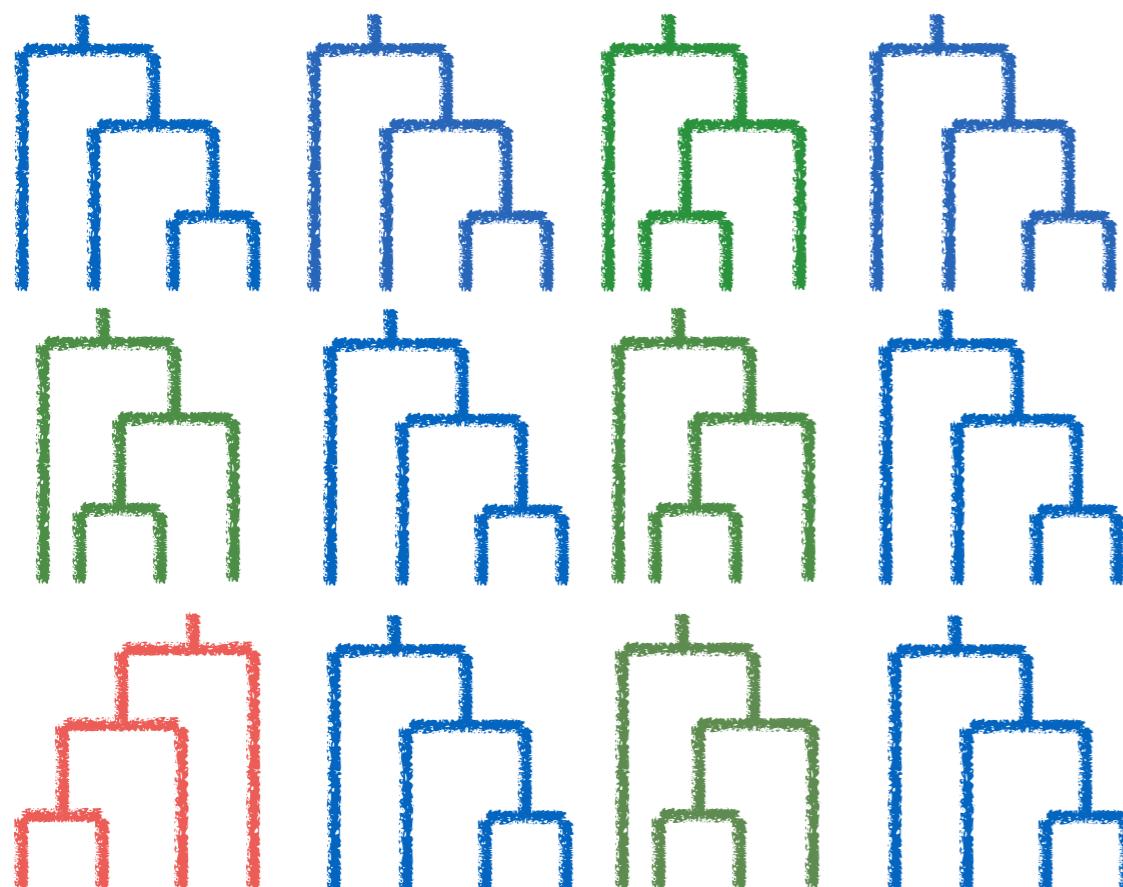
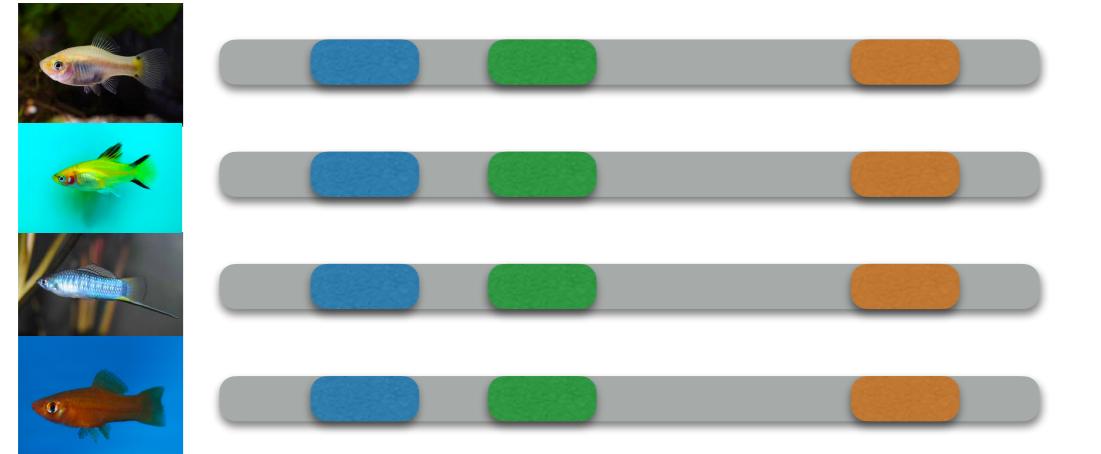
(S.-L. et al, 2017, MBE)

snaQ limitation: Level-1 networks

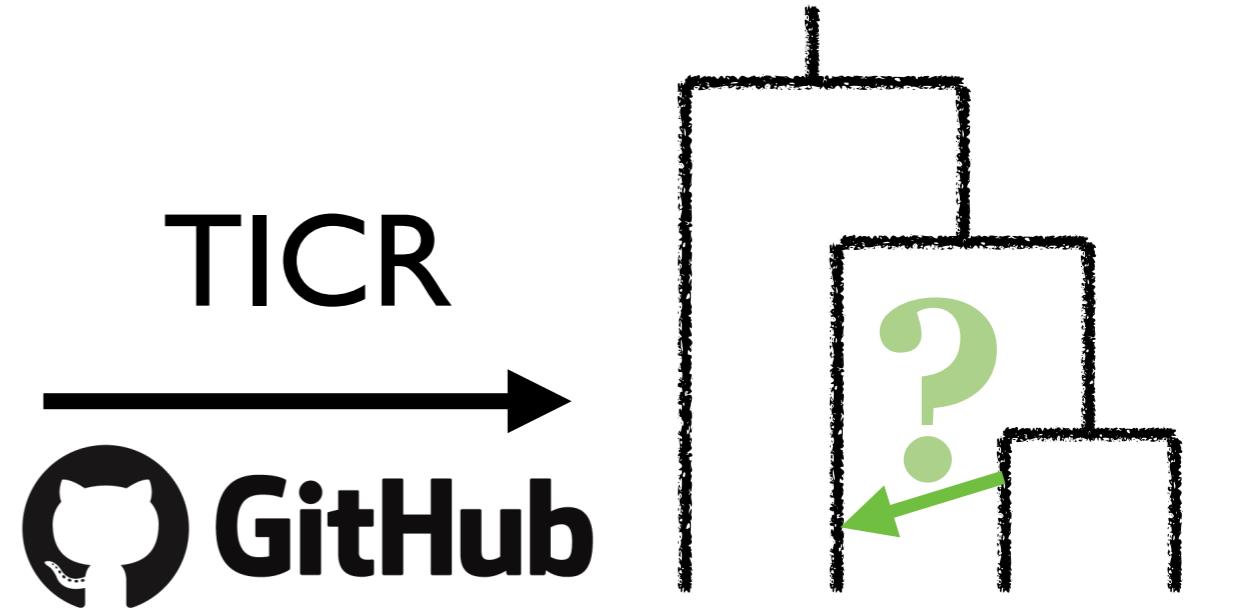


When?

Phylogenetic network



Goodness-of-fit test
Hypothesis test:
Is a tree a good fit?



<https://github.com/nstenz/TICR>
(Stenz et al, 2015, Syst Bio)

PhyloNetworks: analysis for phylogenetic networks

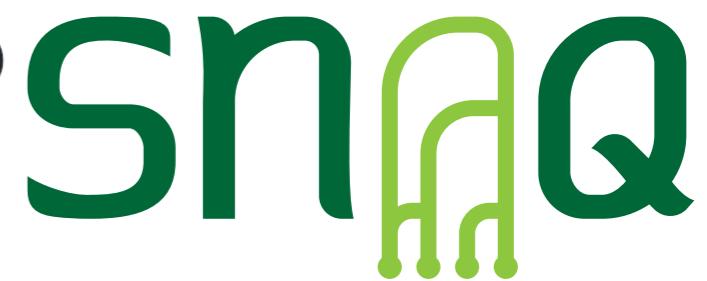
build passing docs stable docs dev codecov 81% coverage 67%

Overview



PhyloNetworks is a [Julia](#) package with utilities to:

- read / write phylogenetic trees and networks, in (extended) Newick format. Networks are considered explicit: nodes represent ancestral species. They can be rooted or unrooted.
- manipulate networks: re-root, prune taxa, remove hybrid edges, extract the major tree from a network, extract displayed networks / trees
- compare networks / trees with dissimilarity measures (Robinson-Foulds distance on trees)
- summarize samples of bootstrap networks (or trees) with edge and node support
- estimate species networks from multilocus data (see below)
- phylogenetic comparative methods for continuous trait evolution on species networks / trees



- Step-by-step tutorial
- Online documentation
- Google user group



(S.-L. et al, 2017, MBE)



<https://solislemuslab.github.io/>



@solislemuslab



crsl4

In-class dynamic

- **Time:** 20 minutes
- **Instructions:** We will go over the PhyloNetworks pipeline which will cover ASTRAL, BUCKy and SNaQ. Create our own reproducible script.
- **Options for you:**
 1. "I think that I can follow the pipeline by myself or with a small group of peers": you should join the Congregate room
 2. "I think I need more one-on-one help to run the commands": you can stay here in the zoom room